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MOTIONS OF THE RUNNING CHEETAH AND HORSE

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The horse is perhaps the most efficient running machine ever evolved; probably no other vertebrate has so many structural adaptations for rapid and untiring progress on the ground. The cheetah is conceded to be the fastest of all animals for a short dash, but lacks the endurance of the horse. This paper will analyze and contrast the running motions of these champions, and will reveal some of the secrets of the cheetah's superlative speed.

Several authors have noted cursorial adaptations of the cheetah (e.g., Pocock, 1927; Hopwood, 1947) but to my knowledge none has contrasted its mode of running with that of other cursorial quadrupeds. Morphological adaptations of the horse have been described by Howell (1944), Eaton (1944), Smith and Savage (1956) and many others. Those references emphasized structure; this paper stresses function. The classical study by Muybridge (1899) has remained the most important analysis of the motion of the horse. A paper by Grogan (1951) provides a concise review of the sequence of footfalls and combinations of supporting members.

MATERIALS AND METHODS

This study was inspired by the excellent film sequence of a running cheetah in the Walt Disney *True Life Adventure* picture "African Lion." I am grateful to Walt Disney Productions for furnishing film strips for analysis.

The photographer, Alfred Malotte, filmed the animal with a telephoto lens, so perspective changes slowly during the run. The chase presented is actually a combination of two dashes: a slower, shorter one, filmed at regular speed, and one taken in slow motion. Sequences of three and seven consecutive strides show the cheetah about side-on to the camera. With a Recordak Film Reader, 155 successive frames were traced. Registration points permitted these to be redrawn as a composite picture, with the images in proper spatial relationship to one another. The film outlines are not sharp, and low vegetation usually obscured the feet when they were on the ground, but there are enough nearly identical frames to establish a ground line and a reasonably accurate depiction of motions.

The analysis for the horse was made from photographs in Muybridge (1899:

171–179) and from the film "Horse Gaits," produced by the Horse Association of America, Inc. In the latter, action was filmed with an electric camera at 128 frames per second; the sequence analyzed shows the horse "Citation" winning the mile-and-one-quarter American Derby in 1948. The method of analysis was the same as with the cheetah.

FINDINGS

Speed.—Figure 1 shows speed records of the horse and, for comparison, of man, for distances up to 900 yards, expressed as rate of travel and lapsed time. Approximate speed of the cheetah is also indicated.

The maximum measured speed for man is 22.28 mph, over 220 yds.; the plotted curve shows that he could average 22.6 mph for 155 yds.

The horse has run ¼ mi. at 43.27 mph; it could probably average 44 mph for 300 yds.

The speed of the cheetah is legendary, yet scantily documented. Authors quote each other and the estimates of lay observers. However, there is both direct and indirect evidence of great speed. Because many artiodactyls will run parallel to a moving vehicle, accurate data are available on the speed of some of them. Einarsen (1948) reported that the pronghorn normally can run at 50 mph, and under favorable conditions can attain 60 mph. On a California desert a pet cheetah overtook a young buck pronghorn (Mannix, 1949). Craighead (1942) stated that the cheetah often runs down its quarry within 150 yds., and that it is not unusual for a cheetah to overtake an antelope that has had a head start of 100 yds. or more.

At Ocala, Florida, John Hamlet includes a cheetah in an animal show featuring species employed in hunting. The cheetah is trained to run in a long enclosure. A popular article (Severin, 1957) reported the results of a speed test stating that "from a deep crouch Okala spurted to the end of the 80 yard course in 2¼ seconds, for an average speed of about 71 miles an hour." Unfortunately, this record must be disregarded because the enclosure is, in fact, about 65 yards long, the method of timing was inexact, and there is an arithmetical error.

It is a general consensus that this remarkable cat can run at least 70 mph.

The speed of the cheetah in the film strips analyzed in this paper could be computed if the film speeds and the animal's body length were exactly known, but these can only be approximated. The studio reported film speeds of about 24 and 48 frames per second; efforts to check these figures with the photographer were unsuccessful. The animal shown is a male. Male cheetahs average about 7 ft. in length (records taken from Hollister, 1918; Shortridge, 1934; Bryden, 1936; Roberts, 1951); the largest of record measured 7 ft. 9 in. Separate calculations based on assumed animal lengths of 6½ and 7¾ ft., and (for the slow-motion sequence) on film speeds of 46 and 50 frames per second give a range of possible speeds between 37½ and 49 mph. Since the animal had to find

its footing among scattered shrubs that were 6 to 24 in. high, these less-than-optimum speeds seem expectable.

Endurance.—Records of animal endurance that are accurate and comparable are difficult to secure. Figure 2 presents some relatively reliable data. The human distance records were taken from various editions of *The World Almanac.* Records for the horse are from the same source and from Howell (1944), who also cited a record (dating from 1853) of 100 mi. at 11.2 mph. If accurate, this is truly remarkable: on the basis of curves plotted from other records one would expect no more than a 9–10 mph rate for this great distance.

Andrews (1933) reported following another perissodactyl, the Mongolian wild ass (*Equus hemionus*), over open country with an automobile. One particular animal ran 16 mi. at an average speed of 30 mph "as well as could be estimated"; the next 4 mi. were covered at about 20 mph. It ran 29 mi. before it stopped from exhaustion. Since it repeatedly changed direction and speed, these figures must be taken as approximate, but it is unlikely that any other

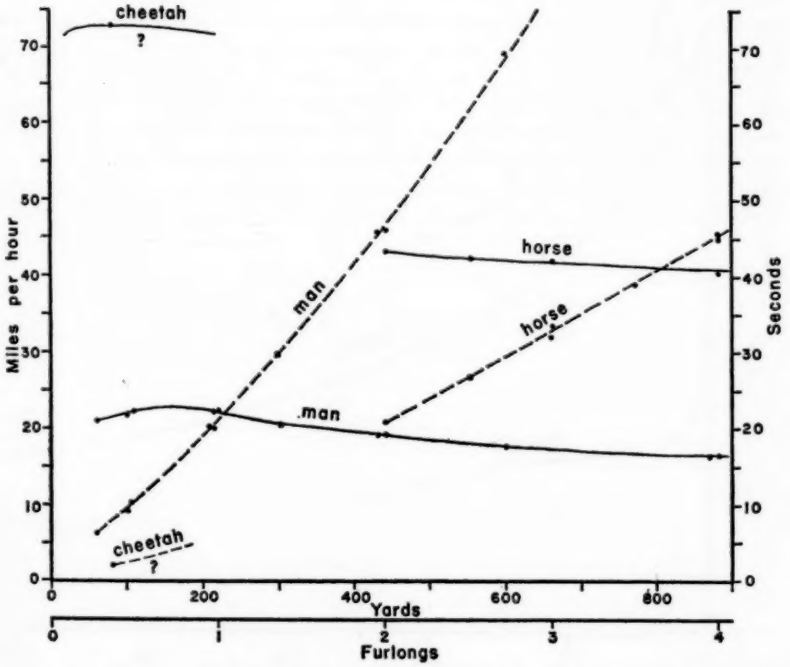

FIG. 1.—Speed records of the cheetah (approximate), horse and man, expressed as rate of travel (solid lines and left ordinate scale) and lapsed time (dashed lines and right ordinate scale). Source for man and horse: several editions of *The World Almanac.*

animal could equal this feat over distances greater than 3 mi. (The pronghorn is faster for short distances, according to Einarsen, 1948.)

In sharp contrast to the equids noted, the cheetah seldom runs more than ¼ mi. Pocock (1927) claimed that 600 yds. is the maximum distance for a chase at speed, and Bryden (1936) stated that two mongrel dogs brought one to bay in 2½ mi. Prey species are almost invariably overtaken by the cheetah, and usually knocked to the ground. However, if they can scramble to their feet and run again, the cheetah often abandons further pursuit.

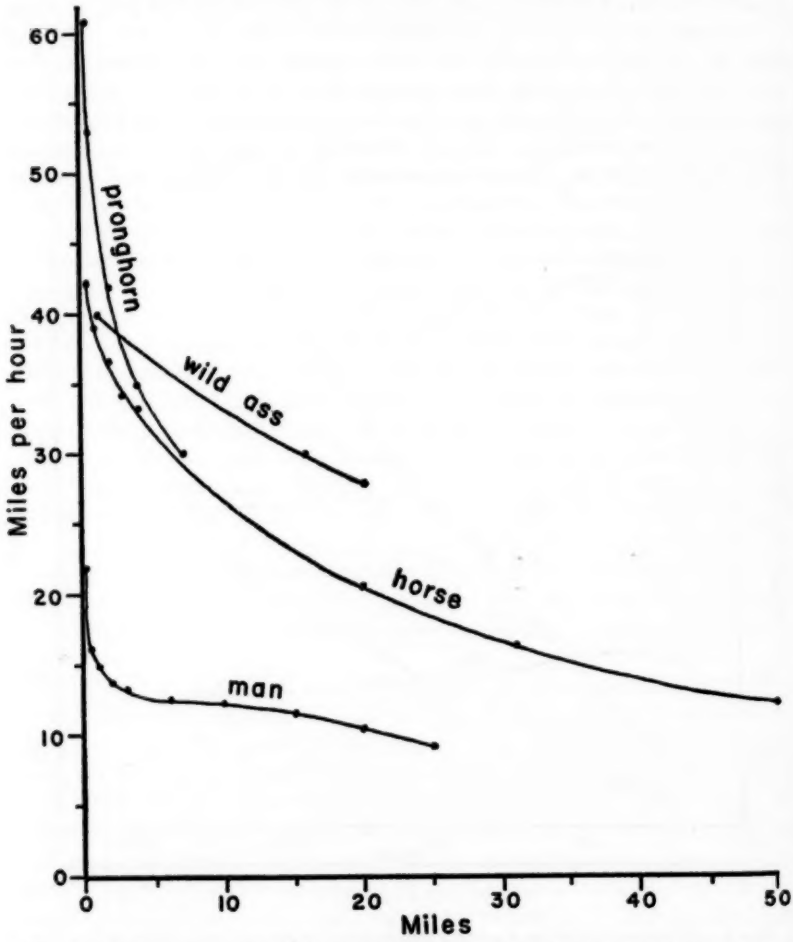

FIG. 2.—Endurance records of the pronghorn, Mongolian wild ass, race horse and man, expressed as average rate of travel for different distances. Sources cited in text.

The longer of the dashes on the film analyzed in this paper was about 325 yds.

Sequence of footfalls.—The leading front or hind foot is second of the pair to touch and leave the ground in each stride or cycle of movement. An unqualified reference to lead applies to the front feet: an animal is said to be running with a left lead if the left forefoot is placed in front of its opposite. I will call the other member of each pair the trailing limb.

In the extreme flexed position the galloping horse passes one hind foot forward of one forefoot (Fig. 4*e*). Since the legs have little lateral motion and nearly equal straddle, the animal can avoid interference only by a sequence in which the leading forefoot is followed with the hind foot on the other side of the body. Thus the front and back legs must use the same lead. This sequence of footfalls, diagrammed in Fig. 3, is termed the transverse gallop.

In the extreme flexed position the cheetah passes both hind feet forward of both forefeet (Fig. 5*h*). To avoid interference it must therefore straddle the forelimbs with the hind limbs. It would seem that the lead of the fore- and hind limbs could be independent, but in practice the leading forefoot is followed by the hind foot on the same side—a sequence of footfalls called the rotary (or lateral) gallop. If the legs on one side of the body were extended as those on the other side were gathered together, and if the spine were flexed to right and left, then the rotary sequence of footfalls would increase the reach of the limbs slightly (about 2 inches per stride for a 7° swing of shoulders and pelvis with a straddle of 8 inches), but this is not the case. Perhaps the rotary sequence provides subtle benefits to balance or muscle function.

The domestic cat commonly places the hind feet nearly opposite one another when running (a gait termed the half bound) but, curiously, it may on occasion follow the horse rather than the cheetah, using the transverse gallop (Muybridge, 1899).

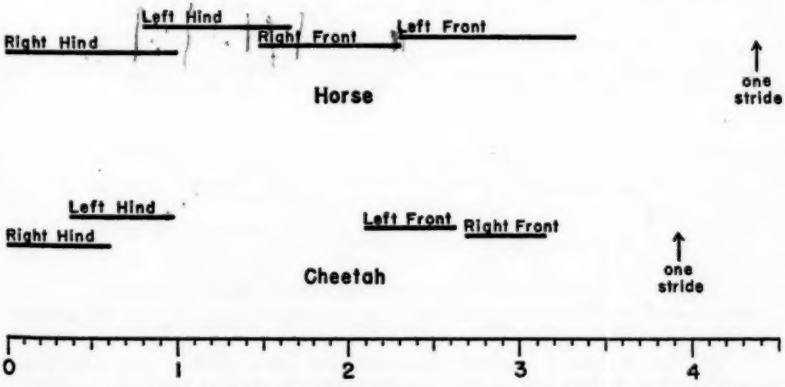

FIG. 3.—Sequence of footfalls and phases of one representative stride, shown in relation to time in tenths of seconds. The period that each foot is on the ground is shown by the length of its respective line.

Phases of the stride and their duration.—The galloping animal has all feet off the ground one or more times in each stride, and during periods of support the legs are used in different combinations. Each suspended period and each combination of supporting members is called a phase. There is much individual variation in the phases of gaits. Indeed, Howell (1944: 222) reported 16 different phase formulas for galloping horses. However, a usual phase formula can be selected for analysis. The nature and duration of the phases of such a formula of the galloping horse and cheetah are shown in Fig. 3.

The horse has all feet off the ground once in each stride—in the flexed position (see Fig. 4*e*). Howell (1944: 240) depicted a light horse that had a second, brief suspended phase, just before the trailing forefoot struck the ground, but this is unusual.

The cheetah is suspended when flexed, and again when extended. I believe there is sometimes a third, though fleeting, instant of suspension—between falls of the front feet (Fig. 3 and positions *d*, *f* and *h*, Fig. 5). Muybridge (1899: 157) anticipated this circumstance when he wrote, "It is probable that future research will discover—with the horse and some other animals—during extreme speed, an unsupported transit from one anterior foot to the other."

Analysis of Fig. 3 shows that the galloping horse characteristically has one suspended and seven supported phases (the supported transit from one forefoot to the other being almost instantaneous when galloping at good speed). The cheetah has three suspended and five supported phases.

The duration of each phase varies not only with speed but also with the

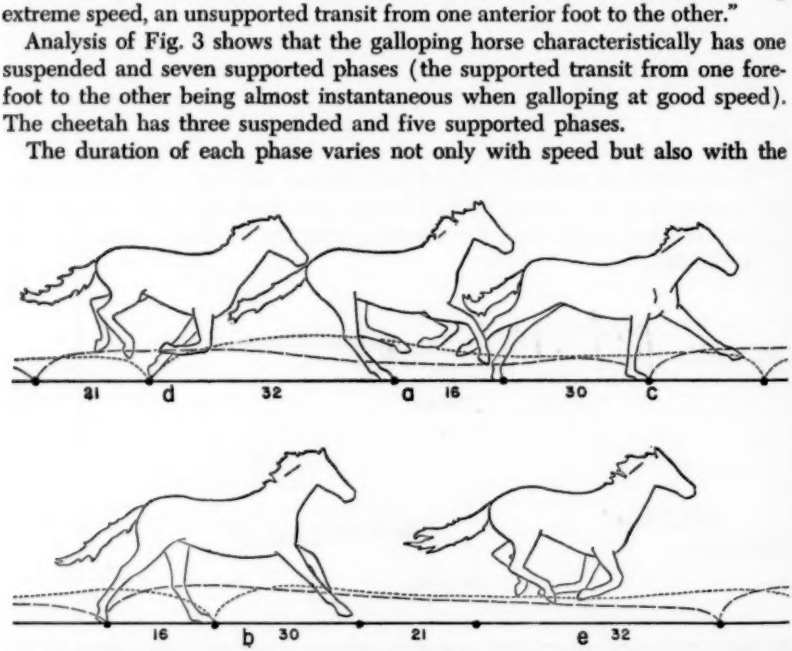

FIG. 4.—Five positions of a galloping horse shown in correct spatial relationship. Trajectories followed by the front feet are indicated above, those by the hind feet below, long dashes for right feet and short dashes for left feet. Positions of footfalls are shown by spots on the ground line. Figures below ground line give for each interval its percentage of total stride distance.

individual and for the same individual at different times. The following statements are as representative as the material available permits, but are only approximations of any particular performance.

When galloping at 35 mph the horse completes one stride in about .44 second, or 2¼ strides per sec.; at about 45 mph the cheetah completes one stride in about .39 second, or 2½ strides per sec. The horse is supported during ¾ of its stride and the cheetah during only half of its stride. Each animal is supported by two legs for 11 to 12 per cent of its total support period.

The trailing hind foot of the horse is on the ground about 85 per cent as long as the leading hind foot, whereas the two hind feet of the cheetah are on the ground about the same amount. The disparity between the animals is greater for the forefeet: the trailing forefoot of the horse is on the ground 80 per cent as long as the leading foot, whereas with the cheetah the foot that has the shorter contact is the leading foot (about 95 per cent as long as that of the trailing foot).

Change of lead.—These differences in duration of support and the asymmetry in resulting stresses require a change in lead from time to time to postpone fatigue. Further, a galloping animal can turn more sharply by leading with the inside forefoot.

Unless rider or terrain demand frequent turning, a horse changes its lead most often to compensate for the relatively great discrepancy in the duration of support provided by leading and trailing legs. Actual lead reversal is usually accomplished first by the forelimbs, but the motion of the hind limbs must be coordinated to avoid the interference that would otherwise result. Probably the spacing of the footfalls must also be altered, and it is likely that average speed will be reduced slightly if the lead is changed frequently.

The cheetah's leading and trailing legs share the exertion of running more evenly, but sharp and frequent changes of direction are usually dictated by the evasive quarry. The cheetah in the film strip changed lead three times in a sequence of 33 strides, and nine times in a sequence of 34 strides. Only once was the same lead used consecutively more than seven times, and five times it was changed after three or fewer strides.

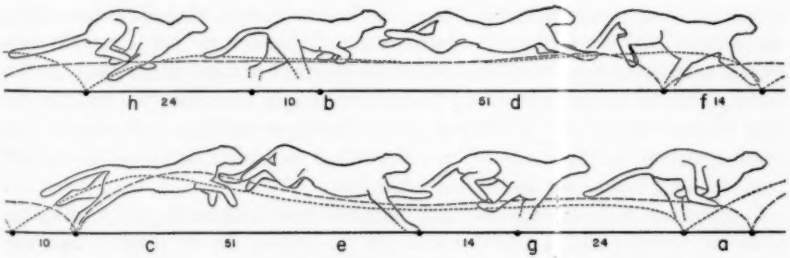

FIG. 5.—Eight positions of a galloping cheetah, shown in correct spatial relationship. Symbols and figures as for Fig. 4.

Several factors contribute to the facility with which the cheetah changes lead, and it is unlikely that speed is sacrificed. In contrast to the horse, there is a time in the stride of the cheetah (just following position *d*, Fig. 5) when the two front and two hind feet are opposite one another in both the horizontal and vertical planes. At this instant the lead can be changed as quickly and smoothly as not, and since this position immediately precedes the placement of the first (trailing) forefoot, the animal need not long anticipate the change of lead required by a turn, and cannot easily be thrown off balance by the dodging of its prey.

Length of stride.—The spacing of footfalls, and hence total length of stride, varies considerably with speed and individual performance. The data presented here are indicative of usual distances. They are based on five strides of three horses and on ten strides of a cheetah.

The strides of the galloping horse recorded by Muybridge (1899) varied from nearly 19 ft. to nearly 23 ft., and averaged 22.8 ft. Exceptional horses are reputed to cover 25 ft. at a stride (Howell, 1944: 241). Assuming the cheetah of the film strip to be 7 ft. long, the shortest of the seven strides traced was 21 ft., the longest 26 ft., and the average 23 ft.

Thus the cheetah covers at least as much ground per stride as does the horse in spite of the great disparity in body sizes: the stride of the cheetah is 8½ to 11½ times its shoulder height (with supporting forelegs vertical), compared with 4½ to 5 for the horse; or 5¼ to 6¼ times its chest-rump length (in position of maximum extension), compared with 3½ to 4 for the horse. The cursorial skill of the cheetah results in large measure from its ability to achieve so long a stride. The number and duration of the suspended phases of its gait contribute; other factors are considered further in following sections of this paper.

In Figs. 4 and 5 the footfalls are marked by dark spots on the ground lines. The per cent of total stride involved in each interval is indicated by the numbers below the ground lines. The most evident difference between the two animals in spacing of footfalls is the greater percentage of stride (51 against 30) that the cheetah achieves between the strike of the leading hind foot and that of the trailing forefoot. At this time it is bounding forward with all feet off the ground; at a corresponding time the horse is supported (compare Figs. 4*b*, and 5*d*). If we arbitrarily eliminate the difference by reducing this particular interval of the cheetah's stride to 30 per cent of total stride (as with the horse) and adjust the remaining three percentages accordingly (making the sum of the intervals again 100 per cent), the horse still has a slightly longer reach between the two hind feet and covers less ground in its suspended transit from leading front foot to trailing hind foot.

Support role of the forelegs.—It has been said that the front legs of a galloping horse do nothing that a wheel would not do better. To be strictly true, the wheel would need to be versatile at banking and at shifting track to maintain the balance of its load, yet support is certainly the principal function of the

equid forelimbs. The hind quarters are closest to the ground when the hind feet are on the ground (see croup-to-ground curve, Fig. 7), but the withers, in contrast, start to rise when the first (trailing) front foot strikes the ground and continue to rise until the leading front foot is lifted. The cushioning of body impact by the digital ligaments (Camp and Smith, 1942) and the muscles that suspend the thorax between the shoulder blades does not prevent the forequarters from rising as they pass over the stiff front legs which are pivoting on the supporting feet. The variation in withers-to-ground height is only 1½ to 2 inches, about one-third of the variation in croup-to-ground height.

It is not possible to determine the deceleration of forward motion that results from the lift given the body by the front legs, but, making some reasonable assumptions, we can learn its order of magnitude. If a 1150-lb. horse galloping 40 mph lifts half of its weight 2 inches as the stiff forelegs pivot forward over the supporting feet, the resulting deceleration will be .034 mph. Conclusion: in regard to speed, a wheel would do nothing for a horse that its front legs don't do just about as well.

Figure 7 shows that the shoulders of the cheetah are falling when the trailing forefoot strikes, continue to fall all the time the front feet are on the ground, and start to rise again only as the first hind foot strikes the ground. Evidently the front legs provide little support and no deceleration, yet, before concluding that the cheetah could run without wheel *or* forelegs, we must consider other functions of its front legs.

Role of the back.—Like other carnivores the cheetah sharply flexes and extends the spine when running. For reasons considered in the next section, the heavy-bodied horse must hold its back nearly rigid, although there is some motion at the sacrum. The amounts of flexion and extension for the two animals, approximated from photographs, are shown in Fig. 6.

The angle that the pelvis makes with the scapula changes about 60° in the running horse, and about 130° in the running cheetah. The rotation of the scapula on the spine is about the same (roughly 20°) in each animal, so the 70° difference between them is attributable to the spine. In both animals the motion of the spine in the vertical plane is greater at the pelvis than at the shoulder.

Of what advantage is a supple spine to a cursorial animal?

One would expect flexion and extension of the spine to increase the swing of the limbs, thus increasing the distances covered during the suspension phases of the stride and extending the duration of the support phases. If this is true, the angles between ground line and limbs as they strike and leave the ground should be more acute for the cheetah than for the horse. The instant of impact of the feet is difficult to determine from the somewhat blurred images of the available moving-picture frames, so I cannot offer quantitative data, but it appears that these angles are indeed more acute for the cheetah.

Swing of the limbs is accomplished for the horse almost exclusively by muscles inserted on the limbs, while muscles of the back also contribute for the

cheetah. This is of significance. If two muscles move one bone on another, the force of rotation is equal to the sum of the individual forces whereas the velocity is limited to that of one muscle acting alone (assuming comparable and adequate leverages and intrinsic rates of contraction). However, if a muscle moves one bone on a second while another muscle moves the second bone in the same direction on a third bone, then there is summation of both force and velocity. Thus, on the recovery stroke, the swing of a limb can be hastened by flexing several of its joints. (Shortening the limb also decreases the load on the muscles.) But when a limb is supporting the body, only a limited amount of motion is possible between the limb joints. Therefore, by swinging its limbs with two independent sets of muscles (of the limbs and of the back) the cheetah increases the speed of its stride.

Although the forward extension of the limbs when the feet strike the ground is only a little greater for the cheetah than for the horse, the more supple spine of the former contributes to substantially greater maximum forward extension before the feet start their backward acceleration preliminary to striking the ground (Fig. 6). Further, comparing the trajectories traced by the feet, as shown in Figs. 4 and 5, it is clear that, in the position of maximum forward extension, the limbs of the cheetah are held higher than are those of the horse. Indeed, they are not only higher relative to body size, but actually higher by about one-third for the front feet and trailing hind foot. It follows that the feet of the cheetah travel farther in moving to the ground. It may be inferred that they have greater backward acceleration when they strike the

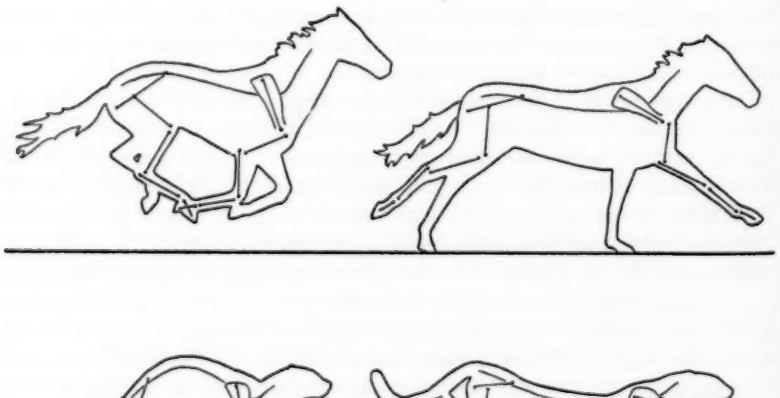

FIG. 6.—The galloping horse and cheetah, shown in positions of maximum flexion and extension of the spine and maximum rotation of the scapula on the spine.

ground and that they probably develop enough traction to prevent any deceleration from factors discussed below and in the next section.

In the flexed position the chest-buttock length of the horse is 80–90 per cent of its length in the extended position (87 in my analysis; 81 in an instance reported by Howell, 1944: 240). The flexed length of the cheetah is only about 67 per cent of its extended length. The actual shortening of the body accomplished by flexion is about 16 in. for the cheetah and 9 in. for the horse. In Fig. 7, changes in chest-buttock length are synchronized with duration of contact of each foot with the ground. For the cheetah, flexion from the position of maximum body length (high points on upper curve) is initiated when the body is unsupported. This helps impart backward acceleration to the front foot that is about to strike the ground. However, any considerable body flexion at this time would tip the shoulders forward and reduce the reach of the leading front leg, so sharp flexion is postponed to the instant the leading foot strikes. Flexion is then rapid, and is nearly completed while that foot is on the ground; only a little more body shortening is accomplished as the leading front foot follows through. Thus the fore- and hindquarters are not significantly drawn toward one another by flexion of the spine: the hindquarters alone move toward the forequarters as the latter are fixed by the forelegs (with reference to the ground, their deceleration is prevented).

In similar manner, extension of the body starts as the trailing hind foot initiates its down stroke. Again this action must help give that foot acceleration to the rear. Some extension also accompanies the unsupported follow-through of the hind legs, but most of the body extension occurs when the hind feet are on the ground. Since backward motion (deceleration) of the hindquarters is thus prevented by the hind legs, nearly all of the increase in body length resulting from extension is added to the length of the stride.

We see that the body of the cheetah moves forward like that of the measuring worm. The added distance is nearly 15 in. per stride, giving an increment in speed of 2 to 2¼ mph at a rate of about 40 mph. What the increment might be at greater speeds will depend on the relative roles played by increased length of stride and increased rate of stride as the animal moves faster. It seems probable that at 60 mph the animal adds in this manner at least 3 mph to its rate of travel.

A limber spine contributes to speed in still another way. As the cheetah's trailing foreleg strikes the ground, its forequarters and hindquarters are moving with equal velocity. But while the front feet are on the ground, the body is flexed on the forelimbs so that, at the instant the leading foot leaves the ground, the hindquarters have greater forward velocity than the forequarters. (The energy necessary to bring this about is here considered to be exerted by muscles of the back and forelimbs, against the ground as traction.) The difference between the velocity of the shoulders and of the center of mass of the entire body is nearly 3½ ft. per sec. when the animal is running at 45 mph. (The figure was derived by estimating the positions of the respective points on tracings

of the animal plotted from successive moving-picture frames and then measuring their relative motion in a known time interval.) In other words, when the forelimbs are on the ground, the portion of the body to which they are joined is moving forward nearly 2½ mph. slower than the body as a whole. Similarly, when the hind feet are on the ground the pelvis is also moving slower than the body as a whole. It is reasonable to surmise that speed is benefited by this circumstance, for it reduces the backward velocity (though not the force) required of the legs in order to propel the body forward.

Body size, speed and endurance.—The speed at which an animal can run is a function of length and duration of stride. Each of these factors is related to body size.

If it were possible to disregard mass, then animals of like form would run at the same speed regardless of body size, because length of stride varies in direct proportion to linear measure whereas intrinsic rate of muscle contraction, and hence rate of stride, varies inversely with linear measure (Hill, 1950).

It is true that the red fox can run as fast as a horse although it is one-tenth as long, but mass cannot be neglected: the horse weighs 100 times as much as the fox, and with like form could scarcely run at all. The force of contraction of a muscle is proportional to the cross-sectional area of its fibers, therefore varying as the square of linear measure. The mass of the body varies as the cube of linear measure, so largeness places the muscles at a disadvantage even when the body is at rest. In motion the disadvantage is greater (Hill, *op. cit.*) because as body size increases the power the muscles can deliver does not quite keep up with the demands placed on them to control the kinetic energy developed in oscillating parts of the body.

To avoid impossible stresses, a large animal must therefore modify the form and function of its body to reduce the load placed on its muscles and supportive tissues. Since momentum is the product of mass and velocity, this can be done by minimizing the motion of one part of the body relative to another, by causing its center of mass to move in as nearly a rectilinear fashion as possible, and by reducing the mass of such structures as must change their velocities. These principles, and related structural adaptations, are noted in publications cited above and in the introduction to this paper.

To run at all, the horse must have a degree of efficiency that assures both speed and endurance. The fox has both speed and endurance for a different reason: its mass is so small that inertia does not increase sufficiently with speed to cause distress. What of the cheetah?

At 125 lbs. the cheetah is only about one-ninth as heavy as the horse, but it is about 14 times as heavy as the fox. *Miohippus*, some litopterns, and many artiodactyls are (or were) of comparable size, but have cursorial mechanisms that conserve energy more effectively than does that of the cheetah. Why is not this cat either smaller or more like the horse in the form of its body and the way that it runs?

The answer is that the cheetah does not need to be efficient; it needs to be

fast, and its size is about optimum for maximum speed. Its muscles can stand the strain long enough for the animal to run the necessary 400 to 600 yds., so greater efficiency is not needed. However, if its body were heavier, then even for such short distances it could not employ every mechanism for gaining speed while disregarding those that improve efficiency. Its speed, then, imposes an upper limit on its body size. There are probably several reasons why the cheetah is not smaller: its size gives it wide vision, independence of irregularities in the terrain, and enough weight to bring down its prey.

SUMMARY

The cheetah is the fastest of animals for a short dash, and the horse has superlative endurance. These animals differ greatly in body size, so it is instructive to compare their ways of running.

Analysis was made from slow-motion moving-picture sequences by tracing images of successive frames and arranging them in correct spatial relation to one another.

The cheetah can sprint at 70 to 75 mph; the horse can attain 44 mph for 300 yds. The cheetah seldom runs more than ¼ mi., the horse can run at 20.5 mph for 20 mi., and its rate

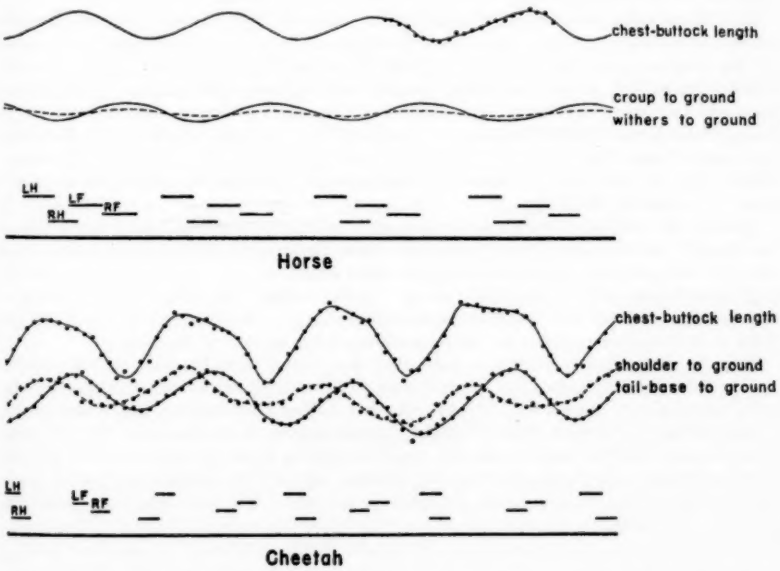

FIG. 7.—Relation of body movement to action of the feet during a little more than four strides. Motion is from left to right. Lower broken lines show, in the manner of Fig. 3, the periods of contact of the feet with the ground; letters *R*, *L*, *H* and *F* mean right, left, hind and front, respectively. Upper curves indicate, by distance above the base lines, variation in chest–buttock length. Middle curves depict height of shoulders (withers) and tail base (or croup) above the ground. All distances above the base line are in proportion to maximum chest–buttock length, which is equated for the two animals.

Summary

of travel declines only slowly as distances increase over 30 mi. The endurance of the Mongolian wild ass is apparently superior to that of the horse.

The horse uses the transverse gallop, usually covers 19 to 25 ft. per stride and completes about 2¼ strides per sec. at 35 mph. Its body is suspended once in each stride, during one-quarter of the stride interval. The leading front and trailing hind limbs support the body longer than their opposites. A change of lead usually occurs first for the front feet, but must be anticipated well before the trailing front foot strikes the ground. The forward motion of the front limbs as they pivot on the supporting feet raises the forequarters, but the resulting deceleration of the body is negligible. Its mass and inertia require that the horse minimize the motion of one part of the body relative to another and move its center of mass in a nearly rectilinear fashion: the feet are not lifted high, there is little up-and-down motion of withers and croup, and the back is relatively rigid.

The cheetah uses the rotary gallop, covers as much ground per stride as the horse, and at 45 mph completes about 2½ strides per sec. The body has two long periods of suspension (and probably a short one) in each stride, adding up to half of the stride. The trailing front foot is on the ground a little longer than the leading foot; the two hind feet have about equal periods of support. Changes of lead are smoothly accompilshed, and can be initiated an instant before the trailing front foot strikes the ground. The front limbs do not raise the forequarters. Body size is about optimum for maximum speed: it is small enough so body form and motion can be adapted for speed with little regard for efficiency, yet large enough to gain a long and rapid stride, as noted below. The feet are lifted high. There is pronounced up-and-down motion of shoulders and pelvis, and marked flexion and extension of the spine.

Flexion and extension of the back contribute to speed by: (1) increasing the swing of the limbs, thus increasing the distance covered during suspended phases of the stride and increasing the duration of the supported phases; (2) advancing the limbs more rapidly, since two independent groups of muscles (spine muscles and intrinsic limb muscles) acting simultaneously can move the limbs faster than one group acting alone; (3) contributing to increased maximum forward extension of the limbs, which permits their greater backward acceleration before they strike the ground; (4) moving the body forward in measuring-worm fashion; and (5) reducing the relative forward velocity of the girdles when their respective limbs are propelling the body.

Speed is the product of stride rate times length. Relative to shoulder height, the length of the cheetah's stride is about twice that of the horse. Factors contributing to its longer stride are: (1) two principal suspension periods per stride instead of one; (2) greater proportion of suspension in total stride; (3) greater swing of limbs, so they strike and leave the ground at more acute angles; and (4) flexion and extension of the spine synchronized with action of the limbs so as to produce progression by a measuring-worm motion of the body.

The rate of the cheetah's stride is faster than that of the horse because: (1) its smaller muscles have faster inherent rates of contraction; (2) its limbs are moved simultaneously by independent groups of muscles; (3) its feet move farther after starting their down strokes before striking the ground, thus developing greater backward acceleration; (4) the forelimbs have a negligible support role and probably actively draw the body forward; (5) the limbs are flexed more during their recovery strokes; and (6) the shoulders and pelvis move forward slower than other parts of the body at the times that their respective limbs are propelling the body.

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PERSONAL NOTICES

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DIFFERENCES IN BEHAVIOR AND TEMPERAMENT BETWEEN TWO RACES OF THE DEER MOUSE

BY DOROTHY DICE FOSTER

Any person who has handled *Peromyscus* in the laboratory will have noted numerous differences in behavior pattern among the various races and species. McCabe and Blanchard (1950), for example, have recorded observations of differences in crouching, hiding and biting among the three species of *Peromyscus* which live in the San Francisco Bay area of California.

The occurrence in Michigan of two sharply distinct races of the deer mouse (*Peromyscus maniculatus*) provides an opportunity to compare the behavior of these two taxonomically related forms.

The prairie deer mouse (*Peromyscus maniculatus bairdi*) inhabits treeless

areas, such as natural prairies, from Michigan west to North Dakota and south to Ohio and Oklahoma (Osgood, 1909). With the clearing of the forests, this race has considerably extended its range to the eastward. In southern Michigan it is common at many places on cleared land and in cultivated fields (Dice, 1932*a*; Blair, 1940; Burt, 1946). It also is common on open lake beaches (Dice, 1932*b*). It completely avoids woods and forests.

The woodland deer mouse (*Peromyscus maniculatus gracilis*) is an inhabitant of heavy woods. Originally its range covered the northern hardwood forests from Quebec south to New York and west to Minnesota (Osgood, 1909). In Michigan it inhabits the forests of the northern parts of the state (Hooper, 1942). From its forest habitat it ranges out into adjacent brushland or marsh (Dice and Sherman, 1922), but it seems never to live in open fields or grassland.

In a few places in northern Michigan the geographic ranges of these two related races, *bairdi* and *gracilis*, overlap, but at no place do both occur in the same habitat. In the laboratory the two races will hybridize, though not readily, and the offspring produced are fertile. No hybrids, however, have been discovered in nature and it is probable that the ecologic isolation due to their habitat differences is usually sufficient to prevent their interbreeding (Hooper, 1942).

In the laboratory these two races of the deer mouse exhibit particularly striking differences in behavior. The prairie-inhabiting race, *bairdi*, appears to be nervous and is rather difficult to handle, while the forest-inhabiting race, *gracilis*, is more placid and is easily handled. Horner (1954) stated that *bairdi* "tend to be timid and nervous. This is manifest in the relatively high frequency of hiding, trembling, chattering of teeth, cowering, and freezing, when exposed to new surroundings. They explore cautiously and slowly at first and, even after they have become familiar with the new environment, perform very deliberately." On the other hand, *gracilis* "are very tractable. Although they bite sharply and struggle vigorously when picked up, they become docile as soon as released. They explore new apparatus spontaneously and with apparent enthusiasm. Their movements are leisurely in contradistinction to the . . . more cautious, deliberate ones of *bairdi*. They exhibit marked curiosity and, even if they become momentarily excited, do not leap blindly from their positions."

The present study attempts to measure the behavior of these two races of *Peromyscus* under experimental conditions which were designed to expose their underlying differences in temperament. The study must be considered as preliminary and exploratory. Few previous attempts have been made to measure psychological attributes in *Peromyscus*.

The Laboratory of Vertebrate Biology supplied the necessary animals and facilities for this study. The facilities of the Statistical Research Laboratory helped greatly in the analysis of the data.

For suggesting the problem and for advice throughout the study, I am indebted to Lee R. Dice. To Francis C. Evans, Norman R. F. Maier and James V. Neel, I express my thanks for advice and criticism. William B. McIntosh and

Elizabeth Barto gave helpful advice and assistance. Dora S. Dice made certain of the measurements and observations and helped in other ways.

EXPERIMENTAL ANIMALS

The laboratory stock of *bairdi* was started with animals caught by Van T. Harris in September 1946 and September 1947 in Washtenaw County, Michigan. The *bairdi* employed in this study were from 6 to 9 generations removed from the wild.

The ancestral *gracilis* were caught by W. Frank Blair in September 1940, in Alger County, Michigan. Some animals caught in the same county by Van T. Harris in September 1947 were later added to the stock (McIntosh, 1955: 7). The *gracilis* used in this study were from 6 to 10 generations removed from the wild.

The experimental animals were provided by and reared in the Laboratory of Vertebrate Biology of the University of Michigan and were given the type of care usually provided there for *Peromyscus* (Dice, 1929, 1947*a*). The matings which produced the experimental animals were always of a single female and a single male. During the years that the stocks have been in the laboratory no selection for mating took place except that close inbreeding was avoided. The male parent was not removed after a litter was born, but remained in the cage with the female and the young.

The young were numbered, marked and removed from their parents usually at the age of about one month. The young males and young females were kept in separate cages. No more than four individuals were ever kept together in one cage after they were of weaning age. Young of different parents were sometimes placed together in one cage.

In addition to the parental stocks of *bairdi* and *gracilis*, reciprocal F_1 hybrid generations were reared and also each of the eight possible types of reciprocal backcrosses between the F_1 hybrids and the parental stocks.

A preliminary analysis of the results suggested the possibility of a maternal influence on behavior. For this reason the reciprocal F_1 hybrids were kept separate at all times during the experiment. The backcross classes were also kept separate by parental type. Genetically the two F_1 classes should be alike. Likewise, the four backcross classes to *bairdi* should be genetically similar. The same, of course, holds for the four backcross classes to *gracilis*.

Animals of both sexes were included in all these classes. The attempt was made roughly to equate the number of males and females within each class. A total of 760 mice were tested. These consisted of 96 *bairdi*, 77 *gracilis*, 183 F_1 hybrids and 404 backcrosses.

The period of testing extended from January 1952 to June 1954. During this period unavoidable breaks occurred in the testing program. The ages at which the mice were tested consequently varied somewhat among the several classes.

METHODS

In order to assess the observable differences in behavior between the two races of deer mice under consideration it was necessary to find objective measures which would define their disparities. Extensive preliminary observation and testing of both types of mice was carried out in order to develop suitable measures. A reasoning maze and an avoidance-conditioning apparatus were experimented with for a time. Comparative observation during handling and in standardized situations gave valuable suggestions. The test items which were finally used were selected because they were effective in differentiating between the races and because they were considered relevant to the underlying racial personality differences. The items are mostly concerned with the animals' behavior in a new and strange situation, the amount of time taken to perform particular acts, and measures of activity. Other acts, such as grooming, biting, somersaulting, tapping and eating were recorded, although the relationship of these activities to the other measures of behavior was mostly unknown. The several measures were incorporated into a testing program to which each mouse in turn was subjected. The analysis of the results included statistical comparison of the measurements from the two races, their reciprocal F_1 hybrids, and the backcross classes.

Apparatus.—The testing equipment employed consisted of an "open-field" apparatus and a two-compartment apparatus with an electric grid. Both of these pieces of equipment were located in a small windowless testing room.

The open-field apparatus was a rectangular box, 38 × 30 inches. Three sides of the box were of hardboard, 20.75 inches high, smooth side in. The fourth side was of beaver board, 14.5 inches high. The mouse was introduced into the field in a transfer container 4.5 × 4.25 × 2.5 inches high which had a remotely controlled door. The container was placed in the middle of one of the long sides of the field.

The top of the apparatus was covered by removable panels of hardboard and included an observation window of glass. Inside the box, six overhead lamps were arranged in two rows of three each, spaced approximately evenly. Five of the lamps were 1-watt neon bulbs. The other lamp, which lighted the door of the transfer container, was a 7-watt frosted bulb. Outside of the apparatus the testing room was completely dark except for the slight amount of light that emerged through the observation window.

The field area contained several objects in addition to the transfer container. Box A, which occupied one corner of the field, was 8 × 4.5 × 3.25 inches high. This box had a door which could be opened by remote control from outside the apparatus. Box B, which occupied another corner of the field, was 8 × 3.25 × 4.5 inches high. Both of these boxes were made of a combination of hardboard, wood, and hardware cloth. In addition to these two boxes, there was a plastic cup, 2.5 inches in diameter at the open end and 2 inches long, which lay on its side and was nailed to a piece of hardboard to prevent its rolling. A watch-glass filled with sunflower seeds and small grains was also placed in the field.

Records of the behavior of the mouse under observation were marked in code by hand on a constant-speed recorder in which the paper travelled 5.8 inches per minute. A guide bar placed transversely across the paper was provided with notches which permitted making records without requiring the experimenter to look away from the animal.

The two-compartment apparatus consisted of a box 16 × 4.5 × 9.5 inches high. A low, metal partition ⅝ inch high divided the apparatus into two compartments, each 8 × 4.5 inches. The back of the apparatus was a pane of frosted glass, behind which was placed a lamp with a 7-watt frosted bulb. This lamp furnished the only light in the testing room during the use of this apparatus. The front of the apparatus was a pane of clear glass, through which the mouse could be observed. The sides were of hardboard. The top of the apparatus was covered with a piece of hardboard as soon as the mouse was placed inside.

The floor of the two-compartment apparatus was a crosswise grid of copper wires spaced ⅜ inch apart. Alternate wires of the grid were connected to give opposite electrical polarities. Alternating current was provided by a transformer operating from a 60-cycle powerline. A potentiometer adjusted the voltage, measured by a voltmeter, to the desired level. A switch operated by the observer turned the current on and off. During that part of the test when the electric shock was used, one compartment of the apparatus was closed off by a partition 6 inches high, restricting the mouse to an area of 8 × 4.5 inches.

Testing procedures.—The mice were tested in two stages. In the first stage an animal was tested always during the afternoon, in the open-field apparatus. The second stage of testing involved the two-compartment apparatus and came on the second morning after the mouse had completed his open-field test. Those mice that were tested in the open field on Friday afternoon, however, did not receive their two-compartment test until Monday morning. Those mice that failed to complete the open-field test on their first trial were retested again two or three days later. Mice that had had two trials in the field apparatus and still had not completed all items of the test were not given further trials. They then were tested in the two-compartment apparatus on the second morning after their last attempted field test. Thus, there was an interval of not less than 36 hours between the two stages of the test program.

In preparation for testing in the open field, the cage occupied by the animal was removed from its place among the other cages and placed on a table inside a large, open-topped

changing box. This box had a high back and sides and a low front, permiting easy access to the cage, but limiting the freedom of the mouse in case of its breaking free during handling. Usually all the animals in a particular cage, generally four, were tested on the same day. Each mouse in turn was seized near the base of the tail with a pair of long rubber-tipped forceps and removed from the cage. While being held in the air by the forceps, note was made whether the mouse bit the forceps.

The mouse was then placed in an 8-inch ounce glass tumbler, the opening of which was immediately covered with a metal plate. While the mouse was in the tumbler, its ear and toe marks were read for identification of its laboratory number. The tumbler was next placed against the transfer container, the top of the tumbler tight against the closed door of the container. The metal plate covering the open end of the tumbler was then removed. In order to reduce the possible effects of the physical presence of a person, the observer was below the line of direct sight of the mouse. The movements of the mouse were observed in a mirror placed at the back of the changing box.

The door of the transfer container was then opened by a string-operated remote-control device and at the same time a stop watch was started. When the body of the mouse, including its hind feet, had entered the transfer container, the door was closed and the watch stopped. If the mouse had made no move to leave the glass tumbler within the arbitrarily chosen 7.5 minutes, it was returned to its living cage and rescheduled for later testing. If the mouse showed some indication of leaving the tumbler, it was given up to 9 minutes before it was returned to the cage.

When the mouse had entered the transfer container, this was carried into the testing room and placed in position in the open-field apparatus. The cover of the open-field apparatus was then put into place, the recorder was started, and the door of the transfer container was opened. Record was made of the elapsed time after door-opening until the mouse came out of the transfer container and of the time until it crossed a semicircular line drawn on the floor 14 inches from the door of the container.

If the mouse had not come out of the transfer container within 10 minutes after the door was opened, or if it had not crossed the semicircular line within 10 minutes after it first left the container, it was removed from the field. The transfer container with the mouse was returned to the changing box and the length of time it took to leave the container and re-enter the glass tumbler was recorded. The mouse was then returned to its living cage and was scheduled for retesting at a later date.

As soon as the mouse crossed the line beyond the door of the transfer container, a stop watch was started. The mouse was then allowed 10 minutes to roam about in the field and to do whatever it wished other than climb out of the box. Record was made of (1) the number of times that the animal climbed upon the transfer container or upon either of the two boxes in the field, (2) the number of times that it went inside the transfer container, and (3) the number of times it investigated the plastic cup. In order to be recorded as having climbed upon any of these objects, the mouse was required to have both hind feet on top of that object. The criterion for investigation of the cup was to have two feet, either hind or fore, upon or inside the cup. Note also was made whether the animal ate any of the seeds available in the dish, how many times it performed grooming acts, and whether it somersaulted.

At the end of 10 minutes the door of box A was opened and the mouse was caught in the transfer container or box A, whichever it happened to enter first. If caught in box A, it was changed to the transfer container before being removed from the field. Only a very few mice would not enter either box within 5 minutes, and these were driven into one of the boxes.

The transfer container with the mouse inside was then taken back to the changing box. The glass tumbler was placed against the door of the container and the length of time noted that the mouse took to leave the transfer container and re-enter the tumbler. If the animal did

not leave the transfer container voluntarily within 5 minutes, it was gently forced out with a wire prod. The mouse was then returned to its regular living cage.

Note was made of the number of fecal boluses eliminated during the whole period of testing, from the time the mouse was first caught, during the time in the open-field apparatus, and until it was returned to its home cage. The occurrence of urination was also noted. The time covered by this period of observation varied among individual mice, depending upon the amount of time taken by each animal in going between the container and the glass tumbler and out of the container into the open field. In the calculations no allowance has been made for this variation in the period of time involved.

For the two-compartment test the mouse was taken from its cage in the same manner as for the open-field test. Again note was made whether the mouse bit the forceps when suspended in mid-air. The mouse was then placed in a 12-ounce plastic tumbler, the open end of which was covered with a metal plate. The mouse was next carried into the testing room and placed in the two-compartment apparatus.

The recorder was started as soon as the mouse was placed inside the apparatus. The stop watch which timed the test was started when the mouse first crossed the middle partition of the apparatus. If the mouse had not yet crossed the median divider within one minute after it was put into the enclosure, the stop watch was started at that time. Beginning when the stop watch was started, the observations were continued for 5 minutes. On the recorder was noted each time that the mouse crossed the middle partition and also each time that it groomed. It was also possible to ascertain from the recorder tracing the length of the longest period of time spent by the animal in one compartment of the apparatus without crossing the middle partition.

At the end of the 5-minute period of the two-compartment test, the partition was inserted in preparation for giving the electric shocks. After placement of the partition there was an interval of 60 seconds before the shocks were started. Shocks of 30-seconds' duration each, followed by rest periods of 45 seconds, were given through a series of five shocks at 5, 7.5, 10, 12.5, and 15 volts, respectively. The reaction of the mouse to each shock was rated on an arbitrary 6-point scale from 0 to 5. The rating of 5 was recorded for the very animated high-step dance characteristic of some of the *gracilis*. Ratings of 4, 3, 2, and 1 were applied to increasingly less vigorous responses, while the 0 rating indicated that no reaction to the shock was detected. Record also was kept concerning somersaulting, attempted wall-scaling, and tapping-grunting during the period of shock testing.

As soon as the series of five shocks was completed the mouse was caught in the plastic tumbler and returned to its cage. This completed the testing of that individual.

Statistical treatments.—Three kinds of data were obtained: dichotomous, continuous, and ratings. Some observations provided dichotomous data, the behavior being present or aspect in each mouse observed. This kind of data was analyzed by a χ^2 test for differences in proportions (Snedecor, 1946: 198–199).

Most of the measures used in this study, however, are of continuous phenomena. These data were treated by analysis of variance. The method used is described in Snedecor (1946: 214–216). Due to the large number of items and of animals, the data were entered on IBM cards and the sums of squares were computed with the automatic computing machine of the Statistical Research Laboratory.

The ratings of the reaction to the electric shock have been analyzed with the same technique used for the continuous data. It is realized that this involves assumptions concerning normality of the distributions and equal intervals between successive ratings. Plots of the distributions indicate the validity of the assumption of normality. In lieu of a method for assessing the spacing between successive ratings in terms of the animals, the assumption of an equal-interval scale is presumed reasonable.

Levels of significance of .05 and .01 have been used in this study. If no significant difference at the .05 level occurred between the parent stocks of *bairdi* and *gracilis*, no statistical analysis was made of the reciprocal F_1 or the reciprocal backcross classes.

A missing measurement, usually due to the non-performance of a mouse in a particular test, has been treated by omitting that animal from the calculations for that measure, consequently reducing N by 1. While this procedure has added a bias to the data, the result is to decrease the chance of falsely indicating a difference between the races. Where, because of retesting the mouse, more than one value has been obtained for a particular measure, the first measurement obtained was used in the analysis.

A graphic plot of the values for those measures which involve time shows that their distribution is skewed. In order to normalize the distribution for the utilization of statistical techniques a logarithmic transformation was consequently used for the following measures: (1) length of time to leave the tumbler and enter the transfer container, (2) length of time to leave the transfer container and enter the field, (3) length of time to cross the 14-inch line in the field, (4) length of time to leave the transfer container and re-enter the tumbler, and (5) the longest time spent on one side of the two-compartment apparatus. The numbers of times that the mice crossed the median divider of the two-compartment apparatus during the two periods of that test were also transformed into logarithms.

MEASUREMENTS AND OBSERVATIONS

Tables of the measurements and observations taken during this study are presented elsewhere (Foster, 1957) and need not be repeated here.

Effects of age.—The ages at which the animals were tested varied somewhat, for it was impractical to test them all at precisely the same age. In order to ascertain the possible effects of age on the measurements, the *bairdi* and *gracilis* parent stocks were divided for statistical analysis into two groups, (*a*) younger than 25 weeks and (*b*) 25 weeks and older, at the time of initial testing.

Between the younger and the older *gracilis* there is a significant difference at the .01 level for two of the measures. More of the older than the younger animals bit the forceps when first picked up prior to testing in the field. Older animals also took less time than younger animals to leave the glass tumbler and enter the transfer container. The differences between the younger and older *gracilis* are not significant for any of the other measures in which there is a significant difference between the *bairdi* and *gracilis* parent stocks. It may be important that the two measures for which there is a significant difference between the two age groups are the first two items in the sequence of tests. Perhaps the younger *gracilis* were more disturbed by the initial handling, but became adjusted in a few minutes so that no difference was evident in the measurements taken later.

For the *bairdi* there is no difference which is significant between the means of the younger group (less than 25 weeks old) and the means of the older group for any measure in which there is a significant difference between the *bairdi* and *gracilis* stocks.

Effects of sex.—In order to ascertain the effect of sex difference, the measurements of the males and females were compared statistically for the two parent stocks. Male *bairdi* defecated more than females during the period of testing in the open field and the difference is significant at the .01 level. This is the only item which exhibited a significant difference between the sexes of either race.

Because the effects of age and of sex on the measurements of behavior were slight, all ages and both sexes in each class have been combined in the following comparisons of the two races and their hybrids.

Tests in the open-field apparatus.—When caught at the base of the tail by the forceps and held aloft, 21 per cent of the *bairdi* bit the forceps compared to 61 per cent of the *gracilis*. In this situation most *bairdi* hung head downward, motionless, with their paws drawn against the body and held rigidly. The whole body was tense. *Gracilis* in the same situation were more relaxed and did not exhibit the rigidity of *bairdi*. On the contrary, most *gracilis* twisted themselves up and around to bite the forceps. Some individuals gained a clinging position on the forceps for a more direct attack. Others, though they established themselves on the forceps, did not bite once they were there. Even those *gracilis* that

continued to hang head downward were not frozen. The difference between *bairdi* and *gracilis* in the proportion of those that bit the forceps is significant at the .01 level.

To leave the glass tumbler and enter the transfer container required on the average 6 seconds for *gracilis* and 36 seconds for *bairdi*, calculated from the logarithmic transformations. Because of the logarithmic transformations these means would not agree with the means taken from the original measurements. The difference in means between *bairdi* and *gracilis* for this measure is significant at the .01 level. Many of the *bairdi* froze when placed in the glass tumbler and did not go into the transfer container in the time allotted. Of 96 *bairdi* tested, 7 did not leave the tumbler, though they were given at least two separate trials. These 7 mice were not included in the statistical treatment for this measure. Many of the *bairdi* that did leave the tumbler did so only after many advances and retreats from the door of the transfer container. The behavior of the *gracilis* was in direct contrast; almost all entered the transfer container as soon as they were aware that the door was open. Usually there was no hesitation at all.

To leave the transfer container and enter the open field required an average of 8 seconds for *gracilis*. The corresponding mean for *bairdi* was 55 seconds. This difference is significant at the .01 level. Seven *bairdi* and one *gracilis* refused to leave the transfer container. These mice are not included in any of the calculations of behavior in the field. Many of the *bairdi* stuck their noses out of the door several times before they came out; some would come part way out and then retreat. *Gracilis*, on the contrary, rarely showed any hesitation in leaving the container to venture out into the field.

To cross the first 14 inches of the open field, once the mouse had left the transfer container, required a mean of 19 seconds for *bairdi* and only 6 seconds for *gracilis*, calculated from the logarithmic transformations. The difference in means between the two parent races is significant at the .01 level. The *bairdi* average was increased by many mice that returned to the shelter of the container before they had ventured far enough into the field to cross the 14-inch line. Some returned to the transfer container and would not leave it again. *Gracilis* only rarely returned to the container between the time when they left it and the time when they crossed the line, usually taking only a few seconds to cover this distance.

Bairdi returned to the transfer container an average of 7.6 times during the 10-minute period of the open-field test, while *gracilis* entered the box 5.1 times. This difference is significant at the .01 level. The difference between the reciprocal F_1 animals is also significant at the .01 level. Both types of F_1 hybrids returned to the container more often on the average than their parents.

Bairdi deer mice climbed up on the transfer container an average of 6.9 times during the 10-minute period of the open-field test, while *gracilis* climbed on the container an average of 16.0 times. This difference between the races is significant at the .01 level.

Bairdi deer mice climbed upon box A an average of 11.6 times during the 10-minute period of the open-field test, while *gracilis* climbed upon this box 14.3 times. This difference is significant at the .05 level.

Box B was climbed upon more frequently by *gracilis* than by *bairdi* during the 10-minute period of testing. *Gracilis* made an average of 9.2 excursions to the top and *bairdi* an average of 7.2. This difference is significant at the .05 level.

The difference between *bairdi* and *gracilis* in the mean number of times during the open-field test that the mice placed two paws on the plastic cup is not significant at the .05 level. The mean for *bairdi* was 8.5, while that for *gracilis* was 9.1.

The number of times that the mouse washed its face or otherwise groomed itself during the 10-minute period of the open-field test differs significantly at the .01 level between the *bairdi* and *gracilis* parent stocks. *Bairdi* groomed on the average 1.4 times during the 10 minutes, while *gracilis* groomed an average of 2.3 times. *Gracilis* were more likely than *bairdi* to eat during the 10 minutes of the open-field test. The animals had not previously been deprived of food, but were offered a preferred food, sunflower seeds, not included in

their regular diet. Some of the small grains, wheat and millet, normally included in their rations were also included with the sunflower seeds for those animals which preferred them. Sometimes it was difficult to be sure whether a mouse actually ate a seed that it picked up. Often it stuffed it into a cheek pouch and carried it back to the transfer container, or in some cases back to its cage. Of the *gracilis*, 76 per cent either ate or picked up a seed during the 10-minute period of the open-field test. The corresponding figure for *bairdi* is 44 per cent. The difference is significant at the .01 level.

A backward somersault is frequently performed by some *gracilis*, but only rarely by *bairdi*. The somersault is performed in several ways, but most commonly is a back flip, which starts from an upright stance on the hind legs. The animal lands right-side-up, facing in the same direction as when starting. The most common variation is the side flip, where instead of turning over completely with the dorsal side toward the floor at the summit of the jump, the animal has its lateral side toward the ground most of the time. Side flippers land in the same position as back flippers. Where there is ample space, the mouse may reach a height about 12 inches above the floor at the summit of the somersault. During the jump it may cover a horizontal distance of about 10 inches. The animal's judgment of the space required is very good and it rarely bumps itself through misjudgment of clearance. None of the *bairdi* somersaulted during the 10-minute period of the open-field test, while 16 of the 76 *gracilis* did. This difference is significant at the .01 level.

To leave the transfer container and go into the glass tumbler after completion of the testing in the open field required 30 seconds on the average for *bairdi*, while *gracilis* took only 7 seconds, both figures having been transformed from their logarithms. This difference between the two races is significant at the .01 level. Of the *bairdi*, 13 refused to leave the container in the 5 minutes allotted, and were not included in the calculations for this item. None of the *gracilis* refused to go from the container into the tumbler in the given time.

Gracilis defecated significantly less during the field testing than *bairdi*. The difference between *gracilis*, with an average of 2.7 fecal boluses, and *bairdi*, with an average of 4.3, is significant at the .01 level.

Bairdi and *gracilis* did not differ significantly from each other in the occurrence of urination during the field testing. The proportions for the two races—*bairdi* (21 per cent) and *gracilis* (22 per cent)—are very nearly the same.

Tests in the two-compartment apparatus.—The series of tests in the two-compartment apparatus started with the observation of forceps biting, just as did the series of tests in the open field. More of both *bairdi* and of *gracilis* bit the forceps in this second series than in the first. The proportion of *gracilis* biters, 65 per cent, is significantly greater than the proportion of *bairdi* biters, 30 per cent.

The longest time that a *gracilis* spent in one compartment of the two-compartment apparatus without moving across the middle divider averaged 25 seconds as transformed from the logarithms. The average for *bairdi* was 53 seconds. The difference between the two races is significant at the .01 level.

The number of times that each mouse crossed the middle divider of the two-compartment apparatus during the first 2.5 minutes differs significantly between *gracilis* and *bairdi*. The data, as transformed from the logarithms, indicate that *gracilis* on the average crossed the divider 29 times, while *bairdi* in the same interval crossed only 7 times.

During the second 2.5 minutes in the two-compartment apparatus, *gracilis* crossed the median partition 26 times on the average calculated from the logarithms, while *bairdi* crossed only 7 times, a highly significant difference. There is almost no difference between the first and second periods in the average number of crossings of the median partition.

Gracilis groomed or washed their faces 2.2 times on the average during the first 2.5 minutes in the two-compartment apparatus. This is significantly different at the .01 level from the *bairdi* average of 1.8 times.

During the second 2.5 minutes in the two-compartment apparatus *bairdi* groomed an

average of 1.4 times and *gracilis* an average of 1.5 times. The difference is not significant. Both races groomed themselves less frequently than during the first 2.5-minute period.

Reactions to electrical shock.—For all five levels of electric-shock intensity, the difference in response between *bairdi* and *gracilis* is significant at the .01 level. The response by *bairdi* was highest at 15 volts, with a mean rating of 1.8. This indicates that at this voltage the mouse usually lifted his feet off the wires, but did not run or jump. The highest average rating for *gracilis* of 4.3 was also for 15 volts. This rating approaches the maximum possible of 5, which indicates extreme activity by the mouse and evident discomfort.

Some *bairdi* avoided the shock for a time by standing on alternate wires, or by bracing several of their feet against the side of the apparatus. The continual somersaulting performed by some *gracilis* when subjected to the electric shock also perhaps served to minimize the duration of contact with the grid.

The amount of electrical stimulus received from the grid undoubtedly varied for each mouse. The amount of dirt and the quantity of hair on the mouse's feet, the degree of dampness of his feet, and other variables may have seriously affected the resistance to the flow of electric current. Also the quantity of corrosion and dirt on the wires of the grid may have influenced the electrical resistance and consequently the intensity of the shock. Before each day's testing, the wires were cleaned with cleansing powder. They also were wiped with a damp cloth after each mouse was tested. These procedures, however, are considered not to have entirely eliminated the differences in the amount of current delivered to the mice.

In spite of the undoubted inequalities in the strength of electrical stimulus applied to the animals, the difference in response between *bairdi* and *gracilis* is very striking. This measure, consequently, may be assumed to demonstrate a fundamental difference in behavioral reaction between the two races.

None of the *gracilis* tapped or grunted during the electric shock. Of the 96 *bairdi* tested, 36 (38 per cent) tapped their feet. The difference in the proportion which tapped is significant at the .01 level.

Somersaulting appeared more frequently under the stimulus of the electric shock than it did during the field testing. Of the *gracilis*, 43 per cent somersaulted as compared with 3 per cent of *bairdi*. The difference is significant at the .01 level.

In the number of attempts to jump or scale the walls of the two-compartment apparatus during the period of electric shock, *bairdi* and *gracilis* differ significantly at the .01 level. Of the *gracilis*, 48 per cent, and of the *bairdi*, 24 per cent exhibited this type of behavior.

DISCUSSION

The measurements and other information obtained in this study permit a critical comparison to be made of certain features of the behavior of the prairie-inhabiting race *bairdi* with that of the forest-inhabiting race *gracilis*. The design of the experiments also has made it possible to search for indications of the possible direct transfer of behavior patterns from parents to offspring in these animals. Evidence is provided that certain racial patterns of behavior are inherited. The most significant results of the study, however, lie in the suggestions which it makes concerning the adaptiveness to their respective habitats of the patterns of behavior characteristic of each of these two races.

Differences in behavior between bairdi and gracilis.—In the experimental situations described earlier in this report, deer mice of the prairie race, *bairdi*, differed significantly from the forest race, *gracilis*, in a number of measurable features of their behavioral responses. During handling, *gracilis* were more likely than *bairdi* to bite the forceps. *Gracilis* took less time than *bairdi* to leave a shelter and enter a new situation, and also returned less frequently to a sheltering container during the time they were in an "open field." *Gracilis* were more active than *bairdi*, as measured by the number of boxes they climbed upon in the open field and the number of times they crossed the middle divider of the two-compartment apparatus. *Gracilis* performed more grooming actions than *bairdi*, were more

likely to somersault and to make wall-scaling attempts, and were more likely to pick up seeds. *Gracilis* defecated less than *bairdi* and were less likely to give the tapping-grunting reaction. The response of *gracilis* to electric shock was very animated in contrast to the "freezing" of *bairdi*.

Certain of these features of *Peromyscus* behavior might be assigned to attributes which in the laboratory rat have been called "timidity" (Bindra and Thompson, 1953) or "shyness" (Hess, 1953). According to this terminology, *bairdi* could be considered to be more timid and more shy than *gracilis*.

The most conspicuous difference in behavior between these two races of *Peromyscus*, however, is the tendency of *bairdi* to freeze when placed in a strange situation or when subjected to stimulus. Most *bairdi* froze for only a few seconds, but some individuals were observed to remain crouched and completely motionless for as long as 4 minutes. *Gracilis* never exhibited the postural rigidity that characterized this response.

This tendency of bairdi to freeze when placed in a strange situation could have produced the statistically significant differences from *gracilis* in many of the measures of behavior here employed. That a greater proportion of *gracilis* than of *bairdi* bit the forceps when picked up by the tail is understandable when it is noted that *gracilis* did not freeze in this situation. The greater length of time that *bairdi*, compared to *gracilis*, took to leave a position and go into a new situation may likewise be interpreted as being in great part due to the tendency of *bairdi* to remain motionless or to move very cautiously in unfamiliar surroundings. In the two-compartment apparatus, many of the *bairdi* froze for a number of seconds, or even minutes, especially when first introduced into the apparatus. Consequently, *bairdi* crossed the median divider less frequently than *gracilis*, which explored the apparatus with no hesitation.

The difference between the two races in their reaction to electric shock was especially pronounced. When subjected to such a shock, *gracilis* tried to escape the painful stimulus by dancing or jumping up and down very rapidly. In contrast, *bairdi* employed its usual defensive response when frightened—it froze. When a *bairdi* did move during the period of exposure to shock, its movements were very restrained and cautious. Only a few of the *bairdi* reacted with the high-step dance which is characteristic of *gracilis*.

The tendency of *bairdi* to freeze when subjected to stimulus must be based on an underlying psychologic difference from *gracilis*. This basic psychologic character of *bairdi* may be called nervous tenseness, although it will readily be admitted that this term is not fully descriptive of the character.

In several other ways besides their tendency to freeze, *bairdi* appeared to be more tense than *gracilis*. Fewer *bairdi* than *gracilis* ate while they were in the open field. *Bairdi* defecated more in the open field than did *gracilis*. *Bairdi* also returned more frequently than *gracilis* to the shelter of the transfer container during the 10-minute test period in the open field, sometimes remaining in this container for considerable periods of time.

The tapping-grunting of *bairdi* is also believed to be a nervous response. In this type of response a front paw rapidly taps the ground, but otherwise the mouse is motionless in the postural attitude associated with the freeze. The grunting sound is usually emitted in association with the tapping. This type of response occurred frequently immediately after the mouse was placed in a new situation, for example, when it had been put into the glass tumbler for the first time. Electric shock elicited the most consistent expression of tapping-grunting. *Bairdi* tapped their feet most often during the period between shocks, rather than while the current was on. No *gracilis* was ever observed either to tap its feet or to grunt.

Consistent with their general tenseness, *bairdi*, in comparison to *gracilis*, appeared to be very quick in their movements. This quickness is expressed not only in speed of movement, but also in sudden changes of direction and in rapid starts and stops. When a mouse is in its cage and the attempt is made to catch it by the tail with the forceps, *bairdi* is much quicker in dodging and more difficult to capture than *gracilis*. A *bairdi* which escapes to the open floor is almost impossible to recapture without the aid of traps; while a *gracilis*

in the same situation can sometimes be caught with the forceps or in the hand. In addition, *bairdi* are very "escape-conscious." When the lid of the cage is lifted, a *bairdi* is likely to attempt a leap through the opening, though it can have no knowledge of where it will land. *Gracilis*, in contrast, never leaps blindly and does not appear to have any intense desire to escape.

Variation between the races in spontaneous activity or exploratory drive possibly might contribute to their observed differences for some of the measures. If the level of spontaneous activity of *gracilis* were higher than that of *bairdi*, for example, this might contribute to the differences observed in such things as number of boxes climbed upon in the open field, or number of crossings of the center of the two-compartment apparatus in a given period of time. From general observations of the animals, however, *bairdi* appear to be equally or more active than *gracilis*. In activity wheels, *bairdi* exhibit a high degree of spontaneous activity. This race was one of the most active of the several strains of *Peromyscus* studied by Dice and Hoslett (1940). Unfortunately, *gracilis* was not included in their study and a direct comparison of the spontaneous activity of the two races has not been made.

Exploratory drive seems to be exhibited about equally by *bairdi* and *gracilis*. This conclusion from general observations in the laboratory is supported by a brief study made in a reasoning maze. In the preliminary stage of thoroughly acquainting each mouse with the maze, which had three separate runways, records were kept of those runways that a mouse traversed during his exploration of the apparatus. When first introduced into the maze, *bairdi* moved more slowly and cautiously than *gracilis*. After a mouse had been in the maze long enough to accustom it to the situation, however, there was no consistent difference in the number of runways traversed in a given time by *gracilis* compared to the number traversed by *bairdi*. Both kinds of mice ran rapidly throughout the entire maze.

The evidence presented here suggests that *bairdi* differs in temperament from *gracilis* chiefly by being more tense. This nervous tenseness of *bairdi* is exhibited especially by the tendency of the animals to freeze when they are startled or when confronted with a strange situation. In certain responses *bairdi* could be said to be more timid or more shy than *gracilis*, but these terms seem to apply to more superficial aspects of temperament than what I imply by the use of the term "tense." The term "emotionality" seems to be used by Hall (1934) for very much the same underlying features of temperament as those here called nervous tenseness. With our present meager knowledge, however, neither of these terms is adequate to describe the fundamental racial differences in temperament.

The differences in behavior between *bairdi* and *gracilis* may be suspected to have a physiologic basis, perhaps related to certain hormones. The studies of Richter (1952) suggest that variations in the secretions of the adrenal glands may be an important factor in producing differences among individuals and races in behavior and temperament.

Possible social transfer of racial behavior patterns.—The differences in behavior between *bairdi* and *gracilis* are evidently transmitted in some manner from generation to generation. Reports concerning the behavior of field-caught deer mice indicate that they exhibit the same racial differences in behavior pattern as animals born and reared in the laboratory. The racial differences in behavior between the two races must consequently have been transmitted through the six or more consecutive generations that the animals have been in the laboratory.

The differences in behavior between the two races here described and in part measured must, therefore, be due either to the transfer of behavior patterns from generation to generation through learning, to differences in heredity between the races, or to both.

Under the conditions of this study all the experimental mice were reared under the same laboratory conditions and were handled in the same way. Both parents were with the young until weaning. The fathers have been noted by Horner (1947) to aid in the care of the young and opportunity consequently is given for certain features of behavior to be learned from either or both parents.

If the racial pattern of behavior in the deer mouse is acquired from the mother, either

by imitation or training, then it would be expected that for each of the measures concerned the means of the two types of reciprocal F_1's would differ from each other and that both would differ significantly from their paternal parents while showing a close similarity to their maternal parents. This is actually true for 3 measures: (1) eating in the field, (2) tapping-grunting during electric shock, and (3) the number of fecal boluses eliminated during field testing. For the first two items the F_1 hybrids differ significantly at the .01 level, while for the third item the significance level is .05. For all three measures the means for the two reciprocal F_1's are similar to those of their maternal parents.

Maternal influence on behavior type, if effective, should also produce a difference between certain of the reciprocal backcross classes. Each backcross class should resemble its maternal parent rather than its paternal parent. However, there are no significant differences in means between any of the reciprocal backcross pairs for either eating in the field or tapping-grunting during electric shock. Instead, much inconsistence appears in the trends shown for these measures by the several classes of backcrosses. For the number of fecal boluses eliminated during the field testing, the trend toward the maternal parent found in the F_1's is sustained in the appropriate backcross pairs, but there are no significant differences between the pairs. This character is not one which would be expected to be learned by imitation or acquired through training.

The possibility of a maternal influence on the behavior of these deer mice is consequently not supported by these measures.

Paternal influence on racial type of behavior is suggested by one measure, biting the forceps when picked up by the tail prior to testing in the open field. The means of the reciprocal F_1 hybrids differ significantly for this measure. Both types of F_1 hybrids also differ significantly from their maternal parents. The backcross mice of type $b \times bg$ bit the forceps significantly more than those of type $b \times gb$. This is contrary to the trend in the F_1 hybrids. No significant differences are exhibited by the other three pairs of reciprocal backcrosses. Furthermore, when picked up by the forceps to be placed in the two-compartment apparatus, the proportion of biters did not significantly differ between the two types of reciprocal F_1 hybrids. This measure consequently fails to demonstrate paternal influence on racial behavior.

For six other measures the reciprocal F_1 hybrids differ significantly: (1) number of returns to the transfer container during the open-field test, (2) longest time that the mouse stayed on one side of the two-compartment apparatus without crossing the median barrier, (3) number of times the mouse crossed the barrier during the first 2.5 minutes in the two-compartment apparatus, (4) number of times the mouse crossed the barrier during the second 2.5 minutes in the two-compartment apparatus, (5) rating of the reaction to shock of 10 volts, and (6) rating of the reaction to 12.5 volts. The reciprocal F_1 hybrids differ significantly at the .01 level for the first three items and at the .05 level for the last three.

For the first of these measures, the number of returns by the mouse to the transfer container during the open-field testing, the means of both types of F_1 hybrids exceed those of both parent stocks, though the $g \times b$ hybrids do not differ significantly from *bairdi*. The means of the backcross pairs, however, are inconsistent in trend. This measure consequently provides no evidence for parental influence on behavior.

The other five measures likewise fail to support the hypothesis of parental influence on behavior. While the means of both classes of F_1's for these measures are closer to the paternal than to the maternal parent, the means of both classes are also closer to the *gracilis* than to the *bairdi* parent stock. Between the reciprocal backcross pairs only one differs significantly and this one is not appropriate to test the hypothesis of paternal influence. The reciprocal backcross pairs for all these items are inconsistent with regard to either a maternal or paternal trend. None of these items consequently supports a hypothesis of either maternal or paternal influence on the behavior of the offspring.

For the other 17 measures, besides the 9 already considered, there is no significant difference between the means of the reciprocal F_1's. This indicates that if training is operative in the transfer of behavior to the offspring, both parents are influential. For some measures the

relationships which would be expected, if learning were effective, were found, with the means of the F_1's intermediate to those of the parent stocks, and the means of the backcrosses intermediate between those of the backcross parent and those of the F_1 hybrids. For some of these items, however, the means for both F_1 hybrids are closer to the mean of the *gracilis* stock than to that of the *bairdi*, indicating that the *gracilis* parent, whether mother or father, had the greater influence. For other measures the means of the backcross classes are inconsistent with respect to the trends found in the F_1's.

Opportunity for *Peromyscus* to learn complex types of responses is lacking in the laboratory, unless one is willing to assume a higher level of communication between parent and offspring than generally is credited to these animals. Harris (1952) found that, under experimental conditions in the laboratory, *bairdi* individuals exhibited a preference for an artificial habitat containing tufts of narrow paper strips, simulating clumps of grass, while *gracilis* preferred a habitat containing tree trunks. The transmission from parents to offspring through any kind of training of the appropriate response to prairie or to forest is difficult to imagine.

Evidence is lacking that among the rodents in general parents directly train their offspring. Munn (1950: 5), in his review of rat behavior, notes the absence of evidence for the transmission of behavioral patterns through parent-offspring learning. Past experiments with rats bearing on this subject have been almost completely negative. King and Donaldson (1929) placed the young of wild rats with tame albino foster mothers. The animals so reared were somewhat more tameable than their wild-trapped parents, but they were much wilder than albinos similarly raised. Stone (1932) reports that young from wild and albino parents behaved like their genetic parents rather than like the foster parents that reared them.

This study likewise fails to find evidence to support any hypothesis of transfer of behavioral traits from generation to generation through learning from the parents. Any consistent indication for maternal, paternal, or joint influence of both parents on the behavior of their offspring is lacking for the several measures employed in this study.

Heredity of racial behavior patterns.—The particular features of *bairdi* and of *gracilis* behavior described in this report have been maintained through the six or more generations that the animals have been bred in the laboratory. No evidence could be discovered for the direct transfer of these racial traits from parents to offspring through social influences. The racial traits measured in this study must consequently be considered to be transmitted through heredity.

That heredity is an important controlling factor in the behavior of other rodents has been demonstrated by numerous investigators. Strains of laboratory house mice, for example, differ in various features of their behavior (Grüneberg, 1952: 208–11). Bagg (1920) early noted considerable differences in habit formation among strains. Lnidzey (1951) reported that five inbred strains exhibited more variation in "emotionality" than could reasonably be accounted for by chance. His conclusion was that the behavior noted was related to genetic determinants. Thompson (1953) likewise noted significant differences in behavior among strains of house mice.

In the laboratory rat, numerous features of behavior are characteristic of particular strains. Strains can be developed by selection which differ in such features as maze-learning ability, spontaneous activity, or "emotionality" (Munn, 1950). Wild rats differ in numerous features of behavior from domestic rats (Richter, 1952). Susceptibility to audiogenic convulsions also differs between strains (Maier, 1943).

Although the major features of deer mouse racial behavior undoubtedly are inherited, it is not suggested that all features of the behavior of these animals are due to heredity alone. Considerable variability in behavior occurs among the individuals within each race. The amount of this variability is indicated by the large standard deviations for certain of the measures. Some of this variability probably is due to genetic heterogeneity within the races, but part also probably is due to the influence of differences among the individuals in personal experiences, nutrition, and state of health.

The mode of heredity of the features of *Peromyscus* behavior described in this report cannot

be ascertained from the information now available. The several measures cannot be related to single genes. The measurements of the F_1 hybrids and of the several types of backcrosses clearly indicate that the mode of heredity of the behavior pattern is not genetically simple in these animals. For practically all the measures, the F_1's are intermediate between the parent stocks. The backcrosses likewise are generally intermediate between the F_1 and the respective backcross parent.

The genetic results of this study, therefore, are concordant with a multifactorial hypothesis of heredity (Mather, 1949) for the several behavioral traits described. This hypothesis assumes that many characters, such as the behavior types considered here, are controlled in heredity by the combined operation of numerous genes, most of which lack dominance and are additive in their effects. The data obtained in this study, however, are not adequate for a critical analysis of the several assumptions made in the multifactorial hypothesis. Consequently, no attempt has been made to estimate the number of gene pairs which control any of these measures of behavior.

In spite of the fact that the precise mode of heredity is not known for any feature of deer mouse racial behavior, the evidence is very strong that at least the major features in which *bairdi* and *gracilis* differ in behavior are inherited.

Ecologic significance of the racial differences in behavior.—The behavioral responses of the animals used in this study are assumed to represent at least fairly well the behavior of the respective wild populations of which they are laboratory-bred samples. Some reduction in genetic variability, however, undoubtedly has taken place due to the small amount of unavoidable inbreeding which has occurred during the six or more generations the animals have been in the laboratory. That life in the laboratory does not in itself alter certain important behavior patterns in *Peromyscus* has been demonstrated by the studies of Harris (1952).

The grass and herbs of the prairie, which is the natural environment of *bairdi*, provide little protection for a mouse against the onslaught of a large predator, such as an owl or fox. Although *Peromyscus* are mostly nocturnal in habit, certain of their predators, such as owls, use vision at least in part in capturing them (Dice, 1947*b*). In this situation the value of the *bairdi* freezing response when alarmed is apparent. In a situation where there is little to hide under, an animal is most inconspicuous when motionless, especially if protectively colored. It is to be noted that the dark coloration of the upper parts of *bairdi* closely matches the color of the soil upon which the animal lives. When a *bairdi* does move, he usually runs quickly until he reaches cover of some sort. These behavior traits, remaining motionless for a time when startled and then suddenly running, make effective use of the animal's protective coloration as well as of whatever natural protection the habitat offers. These behavior traits may be assumed to be important for the survival of the animal and to have obtained their prominent place in the behavioral repertoire of the mouse through the effects of natural selection.

Gracilis is a semi-arboreal animal which spends part of its life on the trunks and branches of trees and shrubs, although it often travels on the ground. Its nests are known to be sometimes built above ground. Presumably it engages in food gathering among the limbs and branches of trees as well as upon the ground. Its buffy coloration is well adapted for concealment on tree branches or among fallen dead leaves. Its runways on the ground often run beside or under fallen logs, which provide some protection from predators.

The animals are perhaps most exposed to the attacks of predators when they are climbing among the branches of a tree or shrub. In such a situation a precipitous movement or a frenzied dash for shelter might result in a damaging fall to the ground. *Gracilis*, however, never make jumps or sudden violent movements, but on the contrary move fairly rapidly but deliberately among the branches. The long tail of *gracilis* has been shown by Horner (1954) to be of great value as a prehensile organ and for maintaining balance when climbing. The actual survival value of the *gracilis* pattern of behavior can only be conjectured, due to the lack of detailed knowledge of the habits of the animals in their natural environment. It may be assumed, however, that the deliberate and steady movements characteristic of *gracilis* are an adaptation to the conditions of its semi-arboreal life.

If it can be assumed that any appreciable part of the variability in behavior among individuals within a population is due to hereditary factors, abundant material would be available in every *Peromyscus* race to serve as a basis for the action of natural selection. Any individual which behaves in a manner unadapted to his particular habitat would be likely to be eliminated early in life. On the other hand, those individuals which exhibit behavior well adapted to their ecologic situation would have the best chance to survive and to leave offspring.

No evidence is available that natural selection actually is effective in any habitat for the evolution of any behavioral trait of *Peromyscus*. Nevertheless, appropriate behavior must be extremely important in the evolution of *Peromyscus* races. The considerable variability of behavior which exists within *Peromyscus* populations provides a favorable basis for rapid evolution in behavior and temperament whenever conditions make such evolution desirable.

SUMMARY

1. When tested in an open-field apparatus and in a two-compartment apparatus the prairie-inhabiting race *bairdi* exhibited significant differences from the forest-inhabiting race *gracilis* in a number of measurable features of behavior.

2. No consistent effects of age or sex on any measure of behavior could be demonstrated among the mature mice of these two races.

3. Much variability occurs in both races in the measurements of behavior, as is indicated by the relatively high standard deviations.

4. The ranges of all the measures of behavior overlap broadly and the racial differences are specified only by the differences between their means.

5. The evidence here presented suggests that *bairdi* differs in temperament from *gracilis* by being more tense. This nervous tenseness is exhibited especially by the tendency of *bairdi* to freeze when startled or when confronted with a strange experimental situation.

6. Comparison of the reciprocal F_1 hybrids between the two races and of their reciprocal backcrosses fails to demonstrate an influence of either parent on the behavior of its offspring.

7. The fact that the two races have maintained their characteristic differences in behavior during the six or more generations that they have been reared in the laboratory indicates that their distinctive behavior patterns are inherited.

8. For most of the measures of behavior employed in this study the means of the F_1 hybrids are intermediate between the means of the parent races. The means of the backcrosses are likewise intermediate between the means of the F_1 hybrids and the backcross parent.

9. The genetic results of this study are concordant with a multifactorial hypothesis of heredity for the several measures of behavioral traits.

10. The tendency of *bairdi* to freeze momentarily or for a longer period of time when alarmed may be assumed to be of adaptive value in its natural prairie habitat. The deliberate and steady movements of *gracilis* likewise may be assumed to be adapted to its semi-arboreal habits.

11. The considerable variability within each of these two races in all measures of behavior indicates that abundant material is available for the operation of natural selection of behavior traits. It may consequently be assumed that adaptive behavior can evolve rapidly in any situation where a change in behavior would aid in adjusting a population to its local ecologic conditions.

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THE SPECIFIC STATUS OF THE NEW WORLD RED FOX

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The relationship of the Old World red fox, *Vulpes vulpes* Linn., of Europe and northern Asia to the North American red fox has long been in dispute. Desmarest (1820) considered that they constituted separate species, *Canis vulpes* Linn. in Europe and Asia and *Canis fulvus* in North America. However, since he based his distinctions on incorrect material—the skull of *C. fulvus* really being that of *Urocyon cinereoargenteus* and the skin possibly from an imported European red fox—his reasons for separating the two forms are not correctly founded, and are therefore invalid. Some workers have since followed his lead in considering that the North American form was specifically different from the European (De Kay, 1842; True, 1884; Bangs, 1897; Miller, 1900; Merriam, 1900 *a*, 1900*b*), and at times distinguished as many as ten distinct North American species. Other workers (Bobrinsky *et al.*, 1944; Ellerman and Morrison-Scott, 1951) have not agreed with this distinction, considering the North American and Eurasian forms to be conspecific, the geographic variants in America thus being races or subspecies of *V. vulpes*. Merriam even changed his opinion in this matter, considering in 1882 that the North American red fox was conspecific with the Eurasian form, and in 1900 that it was not. In this paper evidence will be presented that the red foxes of the Holarctic regions are conspecific with *Vulpes vulpes* Linn.

The red fox in North America prior to Columbus.—The situation is further complicated by the records of introductions of European red foxes into New York, Maryland and Virginia in colonial times. This has led to speculation on the effect of these introductions upon the indigenous red fox populations. The conclusions reached range all the way from absolutely no effect to the complete replacement of the eastern population by the introduced form. It has therefore been suggested that the eastern form, usually referred to as *Vulpes fulva fulva*, was in reality only introduced *Vulpes vulpes vulpes* from Scandinavia, or more likely *Vulpes vulpes crucigera* of the British Isles and France. Rhoads (1903) stated that "In earlier colonial times [the red fox] was unknown in the austral zone, its primitive distribution being greatly altered

by its introduction into the austral habitat by fox-hunting man and by the altered environment of our lowlands. Owing to the importation of European Red-foxes into this country in early colonial times, our east American Red-fox is probably a mongrel species to that extent, claiming as we do that there was a specific difference between the two." Other authors quote the Indians as saying that the red fox was not in the land before the coming of the white man (Bartram, cited by Kalm, 1770), and cite the incident of the first killing of a red fox in Perry County, Pennsylvania, when it had to be identified by a Jerseyman who recognized it "as an English Fox." (Doughty and Doughty, 1830.)

The spread of the red fox into lands being cleared for agriculture, as the pioneers moved westward toward the Mississippi and the Great Plains, also obscures the presence or absence of the red fox on the North American continent prior to the arrival of white man. Bachman (Audubon and Bachman, 1854), states that a large part of the country inhabited by red foxes in 1850 was without them 100 years earlier, and that in early times Pennsylvania was the southern limit of the red fox, but that in time it entered Virginia and the mountains of North Carolina, South Carolina, and finally Georgia in 1850. He says that it has replaced the gray fox over much of this range, and also to the west of the Appalachian Mountains.

"In view of these statements," says Rhoads (1903), "and of the fact that European Foxes had been introduced into New England, Pennsylvania and Virginia for sporting purposes by the middle of the 18th. Century (1750), it looks quite likely that the Red-foxes mentioned by Kalm as being found in New Jersey and Pennsylvania in 1770, . . . and those described by Desmarest as coming from 'Virginia' in 1820, were pure descendants of the European Red-fox. In such a case *Vulpes fulvus*, of course, is a synonym of *Vulpes vulpes* (Linnaeus)."

Baird (1857) says, "It is not a little remarkable that there have been as yet no remains of the Red-fox detected among the fossils derived from the Carlisle and other bone caves. The Grey-fox is abundantly represented. . . . Henry (1809) records it once, and then from the prairies of Manitoba. Long (1819–1820), cited by Seton (1925), does not mention it in his journey across the Plains up the Platte to the Rockies, and back down the Arkansas. However, Richardson (1829) calls it "very plentiful in the wooded districts of the fur countries".

Thus the conclusion to be drawn is that a red fox was native to North America north of Lat. 40° N or 45° N, but was either scarce or absent from most of the unbroken mixed hardwood forests, where the gray fox was paramount. The European red fox was introduced into the eastern seaboard area about 1750, and either partially displaced the gray fox in the southern portion of the continent, or interbred with the scarce population of indigenous red fox to produce a hybrid population.

Examination of bone fragments from a number of Iroquois village sites in Ontario revealed quite a large number of gray fox, wolf, and coyote bones, but very few of the red fox. Many of the sites were dated prior to the arrival of Europeans in North America, some being considered 11th century A.D. Some workers have reported the occurrence of red fox bones in Indian sites in Ontario (Peterson *et al.*, 1953; Kidd, 1949; Wintemberg, 1928, 1939) while others have commented on its apparent absence from sites farther to the south (Gilmore, 1946, 1949; Rhoads, 1903). The reported presence of these red fox remains from sites of pre-European date indicates that the animal occurred naturally in North America, and was not first introduced by the immigrating European. It might be noted that many more red fox remains are reported from the earlier sites (10th to 14th century) than are reported from the later sites (15th to 17th century), and that only recently (within the last 50 years) has the red fox become abundant again in southern Ontario. Therefore it seems likely that there was a period of about 500 years during which the red fox was either absent or very scarce in the settled portions of northeastern North America. Rhoads might easily have been right when he considered that the gray fox was the native form for the eastern seaboard areas at the time of the original European settlement, and that the red fox may have been confined to the northwestern parts of the continent, or to the boreal forests of the north.

The questions remaining unanswered now are in what way the European, Asiatic, and North American red foxes differ from each other, and what effect, if any, the introduction of

European stock had upon the indigenous red fox population. To settle these questions as far as possible, comparisons of Eurasian and North American red fox material were made, and the differences noted.

Comparison of North American and Eurasian red foxes.—The material used in this study consisted mainly of skulls and mandibles, plus a few skins, of wild foxes from Europe, Asia and North America, as follows:

EUROPE. Skulls: *Vulpes vulpes crucigera*: Austria—2, England—3, France—4, Ireland—1, Scotland—2; *V. v. silacea*: Spain—2. Skins: *V. v. crucigera*: France—3.

ASIA. Skulls: *Vulpes vulpes bengalensis*: Assam—2, India—1; *V. v. beringiana*: Siberia—7; *V. v. flavescens*: Iran—1; *V. v. hoole*: China—8; *V. v. karagan*: China—3, Siberia—2; *V. v. pusilla*: India—1; *V. v. tschiliensis*: China—1.

NORTH AMERICA. A total of 283 skulls and 86 skins of red foxes were used in this study. The origins of the skulls are given in more detail in Table 1. The skins were obtained from: British Columbia—2, Manitoba—5, Newfoundland—16, Nova Scotia—5, Ontario—42, Quebec—4, Saskatchewan—1, Iowa—1, Utah—4, and Washington—4.

Altogether, 323 skulls and 89 skins were involved in this study. While the samples of skulls from Europe (14) and from Asia (26) were somewhat smaller than desirable, further material or information was not available.

Bangs (1897) and Merriam (1900*a*) both compare the skulls and pelts of the North American and European red foxes. They compare the New England red fox, rather than the Maritime, Newfoundland or Quebec animal, with the European red fox. They state that the North American red fox is smaller and more lightly built, its tail shorter and smaller. These remarks agree with the conclusions reached from a comparison of the skulls, to be discussed more fully in a subsequent paper. With regard to the pelage, they state that the North American red fox has a paler face with more white hairs scattered throughout the background of rust-colored hairs, while the European form lacks this grizzling of white hairs in the reddish areas. The black of the fore and hind feet is also said to be more extensive. The examination of the three European skins showed that there was a grizzling of white hairs over the red areas of the face, as in the North American form, and that the black of the fore and hind feet was about equally extensive in both populations, although the amounts present in different individuals was highly variable. It would seem, therefore, that the coloration of the two populations, when in the red phase, is comparable, although this may not be demonstrated until a more adequate sample of European red fox skins is available.

The occurrence of three main color phases in the red fox (for this reason sometimes referred to as the colored fox) in both North America and Eurasia supports the single identity of the two populations on a genetic basis. Originally, the presence of black (silver), cross and red color phases in the red fox was considered by Iljina (1934) to be the result of but a single genetic factor, but later Warwick and Hanson (1937) showed that a two-factor hypothesis explained the situation more satisfactorily since the double recessive condition of the single factor hypothesis did not breed true. Butler (1945, 1947) supported the two-factor hypothesis and postulated the presence of two mutations toward a melanic form having occurred in North America prior to 1600—one in Labrador or Quebec and the other in Alaska or British Columbia —which he called the Canadian and Alaskan genes, respectively. Since the Alaskan gene is present not only in northwestern North America but also in Scandinavia, European Russia and Siberia, a further consideration is present for concluding that the red foxes of the Holarctic region constitute but a single intergrading population.

Merriam later compares his species *Vulpes alascensis* with *Vulpes vulpes* Linn. of Sweden and northern Siberia, and states that this Alaskan form "appears to serve as a connecting link between *V. vulpes* and the small faced *fulvus* group of eastern North America." The two red foxes are approximately equal in size according to his statements, but the Alaskan form may be distinguished by the rostrum being more swollen immediately in front of the orbits, and more constricted laterally, and shorter and more upturned anteriorly. The bullae are larger, the basioccipital narrower, the zygomata broader and more spreading, the postorbital constriction

less deep, the incisive formen less extensive, the anterointernal cusp of the upper carnassial more prominent and forming a more decided angle with the body of the tooth, and the crowns of the upper premolars usually longer anteroposteriorly.

When adult specimens from Alaska were compared with those from Europe and Asia, it was found that the Eurasian material was generally smaller in these dimensions: total length of skull, mastoid width, zygomatic width, and width across the roots of the upper canines, which disagrees with Merriam's statements paraphrased above. A comparison of the 14 European and 26 Asian *Vulpes vulpes* specimens with 24 adult Alaskan specimens showed some variation from Merriam's conclusions. The auditory bullae were larger in the the Alaskan form, being more highly inflated and elongated in the long axis, while the bullae of the European forms were not as large or as highly inflated. The basioccipital did seem to be narrower in the Alaskan form, possibly because of the larger bullae, the postorbital constriction was less marked in the Alaskan form, being noticeable in the European form, and the teeth were larger and somewhat more closely spaced. The size of the incisive foramen and the character of the anterointernal cusp of P^4 were highly variable, and no differences of the nature suggested by Merriam could be found. The comparisons of the rostra and of the zygomata were found to be insupportable, the construction of the skulls varying sufficiently to include both stout and slim rostra, and zygomata both narrower and wider depending upon the age of the specimen. It was therefore concluded that there were some distinctions between the Eurasian and Alaskan red foxes, involving the total size of the skulls, the bullae, the basioccipital, the postorbital constriction, and the dentition.

A comparison was made of the 14 European *Vulpes vulpes* specimens with 56 skulls of the red fox from eastern North America, and a number of differences became obvious. The European *V. vulpes* differs from the eastern North American red fox in that the rostrum is heavier, the anterior infraorbital margins of the zygomata are more rounded, the anterior frontal areas superior to the orbits and lateral to the median sagittal sulcus are slightly inflated, the canines and incisors are heavier, and the posterointernal talon of the permanent first upper molar, M^1, is more rounded and emphasized. The size of the skull is larger and more massive, the infraorbital foramen is more prominent, and the postorbital constriction is more developed. To the extent that there is the size difference, and the proportions of the snout differ, these conclusions agree with those suggested by Bangs and Merriam.

The 14 European crania were also compared with 54 adult crania from Labrador, Newfoundland and Nova Scotia, since there is a difference between the fox populations of these areas and of the New England states. The two forms proved to be similar in the degree of heaviness of the skull, in the total size of the main dimensions of the cranium and in the relative proportions of the rostrum to the braincase. The teeth were also of approximately the same size, but the zygomata of the European forms were slightly wider than those of the northeastern North American forms in females. The other stated differences distinguishing *V. vulpes* from the New England form still existed and on these bases the European cranial specimens could be distinguished from those from North America.

It was therefore concluded that whatever effect the introduction of the European red fox into eastern North America had upon the indigenous population, it was not sufficient to show up in the sample available from New England, and that the differences that existed between the two forms were maintained when the more northern form was compared with the European form, allowances being made for the differences between the two eastern North American forms. Since the two forms from either side of the Atlantic show these differences, it seems reasonable that they might be correctly ascribed to two separate species, but before taking a decision on this question, it was considered advisable to investigate further the European, Asian and North American relationships.

The possibility of a continuous clinal intergradation in the characters of the red fox from western Europe across Asia to North America and Newfoundland was investigated with respect to the characters of the skull mentioned in the previous paragraphs. All those characters of the skull that had to do with the shape or proportions of the bones of the cranium were

found to vary and intergrade in such a manner as to make it most difficult to express such variation at all accurately on the small sample available from Eurasia, especially when allowances were made for sex and age variation. Consequently, the dentition was searched for a character or characters which showed variation between the two extremes of distribution, as tooth characters are less affected by the environment and are a true reflection of the genetic constitution of the individual. The first character examined was the shape and position of the

CATEGORY I: Note rounded buccal cingulum, broad talon, convex mesial face, and pattern of cusps.	
CATEGORY II: Note bowed buccal cingulum, bowed distal face, narrowed talon, prominent mesial cingulum on protocone, and pattern of cusps.	
CATEGORY III: Note similarity to II, but lack of cingulum on protocone, and incipient cusp between meta- and hypocones.	
CATEGORY IV: Note angle on buccal face, elongated talon, concave mesial and distal faces, and small protoconule.	

FIG. 1.—Occlusal views of four categories of M^1 to show variation. All diagrams are oriented with buccal surface at right, mesial at bottom, lingual at left, distal at top. Arrows indicate points of variation. All approximately natural size.

TABLE 1.—*Number of specimens with M^1 crown patterns of the four different categories; figures in parentheses are percentages of total samples*

AREA REPRESENTED	M^1 CROWN CATEGORIES				N
	I	II	III	IV	
Western Europe	14 (100)				14
Central Asia and India	3 (60)	1 (20)	1 (20)		5
China	1 (6)	9 (81)	2 (12)		12
Siberia	1 (11)	7 (78)	1 (11)		9
Alaska, Yukon and Mackenzie	3 (6)	33 (66)	14 (28)		50
Northern B.C., Alta., Sask., Man., NW Ont.	1 (4)	6 (26)	16 (70)		23
Southern B.C., Washington and Oregon	—	8 (42)	11 (58)		19
Great Basin Area	—	8 (36)	11 (50)	3 (14)	22
Maritimes, Nfld., Lab., and Quebec	—	14 (21)	48 (72)	5 (7)	67
Eastern N. America W of Great Lakes and Mississippi	—	6 (12)	28 (61)	12 (27)	46
Eastern N. America S of Great Lakes and E of Mississippi	—	2 (4)	17 (30)	37 (66)	56

anterointernal cusp of the upper carnassial, a character first mentioned by Merriam (1900*a*), but although variation was found to exist in this character, it was not sufficiently stable to permit setting up categories within different populations for comparison.

A further character was found in the configuration of the talon of M^1. The shape of this part of the crown of the first upper molar differed strongly from Europe to America, and intermediate steps of difference could be seen in the Asian specimens. Four classes or categories of the shape of this talon were arbitrarily set up, the general condition in the western European and eastern North American populations forming the two end categories of the series, while two selected intergrading conditions were chosen as the intermediate forms. These categories are illustrated in Fig. 1. A total of 323 individuals from Eurasia and North America were then examined, and the category of M^1 determined. The results of this examination are shown in Table 1. The figures in this table indicate the actual number of individuals in any one category, while the figures in parentheses following them give the percentage that the actual number represents of the total sample from that area.

Despite the paucity of material from central Asia, and the impossibility of dividing the material from Asia generally into subspecific categories on that account, it is obvious that there is a fairly gradual and continuous shift of emphasis from Type I to Type IV categories as one proceeds eastward across Asia and North America. This shift is so continuous and gradual that nowhere in the series can any definite position be found where the ratios differ radically between two adjacent areas, and where the division between *Vulpes vulpes* and *Vulpes fulva* might be placed. Undoubtedly, when further material is available from Russia and eastern Europe, the slope of the shift will probably be reduced in the upper portion of the table. Such a change would support further the general gradual nature of the change from area to area and thus confirm the impossibility of selecting a natural position at which to divide *V. vulpes* from *V. fulva*.

The gradual change in the character of the talon of M^1 from western Europe to eastern North America across Asia is reflected to some extent in the other characters of the skull, even though these are very difficult to measure or classify. The Alaskan populations differ from the eastern North American populations in the following characters: they are larger, have heavier rostra, some inflation of the frontal region above the orbit, a more developed frontal sagittal sulcus, a more prominent infraorbital foramen, larger teeth, and larger and more inflated bullae. It is

precisely in these characters that the European and Asian animals more closely resemble the Alaskan animals, and by which they differ from the eastern North American forms. Therefore, it seems likely not only that the Alaskan and Eurasian forms are closely linked, as suggested by Merriam, but that they represent an intergrading series extending across the whole Palaearctic region. The characters that Merriam used to distinguish the Alaskan forms from the Eurasian forms (size of rostrum, bullae, etc.) may all be reflections of the slightly increased size of the Alaskan animals, as they seem to be linked with populations of the larger animals in North America.

Conclusion.—As all the evidence discussed above shows that the Holarctic red foxes intergrade from population to population, and as other characters are not available by which the Siberian red foxes can be distinguished from the Alaskan, it is reasonable to consider that this distribution constitutes a single population in which the individuals all belong to a single species. It is therefore proposed that the North American, Asian and European red foxes be considered to be one species, all the presently described forms being subspecies of this single species. This form must be known as *Vulpes vulpes* Linn. and *Vulpes fulva* (Desmarest) must be considered to be a synonym.

SUMMARY

Cranial variation in the North American and Eurasian red foxes was studied with a view to clarifying the relationships of the two continental populations. Specimens of western European and eastern North American origins were contrasted, and found to differ only in minor degree. Comparison of Siberian and Alaskan specimens showed a very high degree of similarity, despite a reduced sample from Siberia. The conclusion reached was that the red foxes of the Holarctic region were all members of a single clinal system of variation running from Europe through Asia to North America. Although the number of specimens from Eurasia was not as large as desired, it was deemed adequate to support the conclusion that the red foxes of North America and Eurasia belong to a single species, and that therefore *Vulpes fulva* (Desmarest) would have to be considered synonymous with *Vulpes vulpes* Linn., as the latter name has priority.

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TAXONOMY OF THE EASTERN PIPISTREL

By Wayne H. Davis

Problems encountered in the subspecific designation of specimens of the eastern pipistrel, *Pipistrellus subflavus*, have long shown the need for a critical taxonomic study of this bat. Such a study, recently completed, indicates a need for certain revisions in the nomenclature applied to this species.

This paper, which represents part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Illinois, is based upon the examination of 1492 specimens of *Pipistrellus subflavus*. Acknowledgment is made for the use of specimens belonging to the following institutions or individuals (abbreviations in parentheses are those used throughout this paper): American Museum of Natural History (AMNH); Carnegie Museum (CM); Chicago Natural History Museum (CNHM); University of Connecticut (UC); Cornell University (CU); Florida State Board of Health (FSBH); University of Florida (UF); W. G. Frum (WGF); University of Georgia (UG); Museum of Comparative Zoology, Harvard University (MCZ); University of Illinois, Museum of Natural History (UI); University of Kansas, Museum of Natural History (KU); Louisiana State University (LSU); University of Massachusetts (MU); University of Michigan, Museum of Zoology (UM); University of Minnesota (MINN); University of Missouri (UMO); New York State Museum (NYSM); North Carolina State College (NCS); Ohio State Museum (OSM); Oklahoma A & M College (OAM); F. L. Osgood (FLO); H. B. Sherman (HBS); Texas Cooperative Wildlife Research Unit (TCWR); Texas Natural History Collection (TNHC); Biological Survey Collections, U.S. National Museum (USNM); J. S. White (JSW); and University of Wisconsin (UW).

Since it was recognized that collectors frequently pick those bats which appear unusual in color as those to be saved for specimens, and the measurements taken by different collectors vary widely in accuracy, it was decided to collect and prepare large random series from different parts of the range of the species being studied. Such series were taken in Wisconsin, Illinois, West Virginia, Oklahoma, Arkansas, Alabama and Georgia.

For each specimen examined all information available on the label was recorded. A series of nine standard measurements was taken from each skin and skull where possible. Notes on color were made. The animal was then classified as to age. Age categories of young and adult were based upon condition of the epiphyses and pelage. Only those recognized as adults were used in the taxonomic study.

After all specimens were examined, measurements were averaged for each locality. Some localities quite close together were grouped as one. Due consideration was given to topographical differences in each case before any grouping was done. Because of possible migrational movements in this species, series taken in summer were compared with those taken in the same region in winter to

see if possible differences could be detected. None was found. Since females were found to be slightly larger than males, the sexes were treated separately in analysis of measurements.

The averages for each measurement taken were placed on separate maps. Each map was then studied for evidence of geographical variation in size.

Color was put on a somewhat objective basis by choosing ten specimens representing the normal range of color variation found in the central part of the range. These specimens were assigned numbers, and all specimens examined were compared to these standards. Figure 1 shows the average color indices thus obtained for samples from different parts of the range. Words used throughout this paper to describe color are common terminology and not standards.

Pipistrellus subflavus subflavus (F. Cuvier)

V[espertilio] subflavus F. Cuvier, Nouv. Ann. Mus. Hist. Nat. Paris 1: 17, 1832.

Vespertilio erythrodactylus Temminck, Monogr. de Mamm. II, p. 237, 1835; not seen by me; after H. Allen, U.S. Nat. Mus. Bull. 43: 121, 123, March 14, 1894 (type from neighborhood of Philadelphia, Philadelphia County, Pennsylvania).

Scotophilus georgianus H. Allen, Smithsonian Misc. Coll. No. 165, Vol. 7, art. 1: 35, June, 1864 (type from Carlisle, Cumberland County, Pennsylvania).

Vesperugo carolinensis H. Allen, U.S. Nat. Mus. Bull. 43: 121, March 14, 1894 (renaming of *Scotophilus georgianus* H. Allen).

Pipistrellus subflavus Miller, N. Amer. Fauna 13: 90, October 16, 1897.

Pipistrellus subflavus obscurus Miller, N. Amer. Fauna 13: 93, October 16, 1897 (type from Lake George, Warren County, New York).

Type Locality.—Georgia ("de Géorgie"). Hereby restricted to the site of the LeConte Plantation, 3 mi. SW Riceboro, Liberty County, Georgia. As the neotype I select an adult female, skin and skull, UI No. 16177, taken July 4, 1957, by W. L. Jennings, original No. 2.

Range.—From central Minnesota and southern Quebec south to Georgia and western Florida, west to southwestern Oklahoma and the Edwards Plateau of Texas, southward into Tamaulipas (see map, Fig. 2).

Diagnosis.—A race of *Pipistrellus subflavus* characterized by reddish tones to the fur, median color range, and medium size. Color variable, ranging from pale yellow-orange and bright orange to dark reddish brown. Underparts vary from pale yellow-orange to dark mahogany.

Comparisons.—From *P. s. clarus*, specimens of *P. s. subflavus* differ in being darker in color and slightly smaller. From *P. s. veraecrucis*, *subflavus* differs in being larger and paler in color. From *P. s. floridanus*, it differs in having reddish hues to the outer bands of the hair and the tips of the guard hairs and in being slightly smaller.

Remarks.—This is a widely distributed race whose center of abundance is the Ohio River Valley. Populations in this large area show very little geographical variation. Those from the caves of northeastern Oklahoma average slightly paler than do others of the race. Specimens from eastern Kentucky, western West Virginia, western North Carolina, eastern Tennessee, and northeastern Alabama average somewhat more reddish than do those from other parts of the range.

The only differences noticeable in size are in those specimens from the Atlantic seaboard. Specimens taken in summer from West Point, N. Y., Morris County, N. J., and the vicinity of Washington, D. C., average slightly larger in length of the forearm and length of the metacarpals than those specimens taken west of the Appalachian Mountains. The specimens from the Atlantic seaboard are more comparable in size to *P. s. floridanus* than to *P. s. subflavus* from the Ohio River Valley.

Specimens from Upper Ward's Cave, Albany County, N. Y., as well as those from Vermont, western Massachusetts, Quebec, and eastern Ontario average slightly darker than specimens from other parts of the range (see Fig. 1). The name *P. s. obscurus* Miller is generally applied to specimens from these areas. Since I can find no features sufficient to distinguish this population, I regard this name as a synonym of *P. s. subflavus*. Miller (1897) described *P. s. obscurus* as being "readily distinguishable from true *subflavus* by its darker, duller, less yellow color. The difference is especially noticeable on the ventral surface, which is generally a rich yellowish wood brown in typical *subflavus*, dull isabella color in *obscurus*." In the present study, specimens from various parts of the range of *P. s. subflavus* were found which were indistinguishable from the darker ones from New York, Vermont and Ontario. Conversely, many specimens from the latter localities were found to fit in with the lighter colored ones from the rest of the range. Color of the ventral surface was generally found to follow the same pattern. The one exception was a specimen from the cave at Fourth Chute, Renfrew County, Ontario (USNM No. 297215), which was found to be darker on the ventral surface than are specimens from other parts of the range. However, this does not seem to be sufficient grounds for retaining nomenclatorial separation for the populations in this region.

Specimens from Tamaulipas show characteristics intermediate between *P. s. subflavus* and *P. s. veraecrucis* and probably represent intergrades between these two races. They are referred here to the race *subflavus* because they show a closer resemblance to it in all characteristics than to *P. s. veraecrucis*.

Specimens from the Edwards Plateau of Texas are not typical of *P. s. subflavus* in that they are paler and less reddish. They seem to be intergrades between this race and *P. s. clarus* but

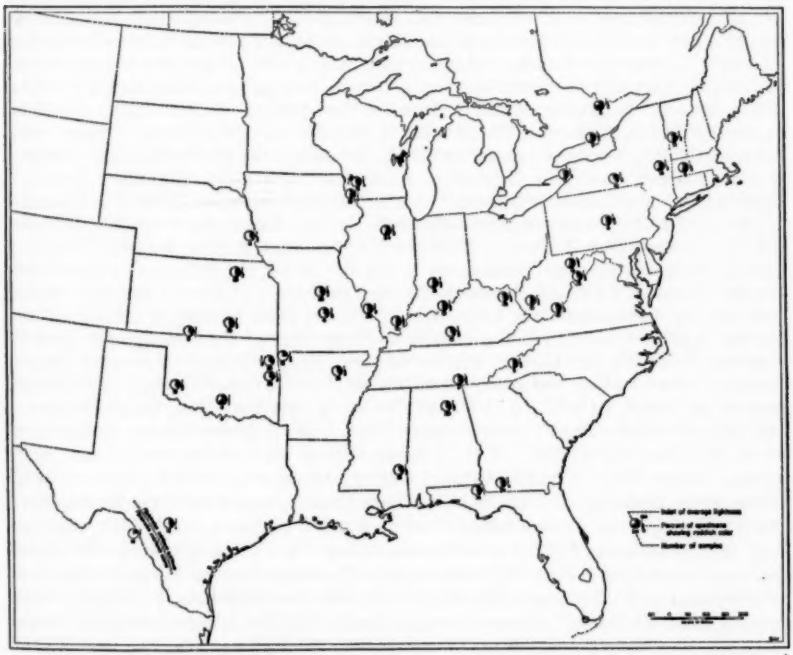

FIG. 1.—Geographical variations in the colors of *Pipistrellus subflavus subflavus* and *Pipistrellus subflavus clarus*.

are usually separable from the latter. They are here referred to *subflavus* because they seem to have a closer affinity to this race than to typical *clarus*.

A specimen from Roswell, Gwinnett County, Ga. (MCZ No. 32140), and one from St. George Island, St. Marys County, Md. (USNM No. 15913), are indistinguishable from specimens of *P. s. floridanus*. These were taken August 8, 1934, and August 20, 1887, respectively. It is possible that *P. s. floridanus*, like some birds and perhaps other southern bats, may wander northward at this time of year. Unless it can be shown that this actually happens, however, it is best that these specimens take the name *P. s. subflavus* and be considered as unusual variants of the populations of the regions in which they were taken.

Measurements.—Average measurements (in millimeters) of 13 males and 10 females from Waterfall Cave, 7 miles north of Cairo, Grady County, Ga., are respectively: total length, 86, 89; length of tail, 40, 41; length of foot, 9.9, 9.7; length of ear, 13.9, 14.1; length of forearm, 33.4, 34.1; length of third metacarpal, 31.7, 32.1; length of fifth metacarpal, 30.0, 31.2; length of tibia, 13.9, 13.8; greatest length of skull, 12.9, 13.0; zygomatic breadth, 7.8, 8.0; breadth of cranium, 6.6, 6.7; height of skull, 5.8, 5.9; alveolar length of maxillary toothrow, 4.1, 4.1.

Specimens examined.—Total number 1302, from the following localities: ONTARIO—*Renfrew County*: cave at Fourth Chute, 2 (USNM), 1 (AMNH), 1 (UM); *Hastings County*: Tyendinaga Cave, Tyendinaga Twp., 2 (USNM), 1 (MCZ); *Welland County*: Point Abino, 6 (KU); QUEBEC—*Wright County*: LaFleche Cave, near Wakefield, 1 (MCZ); MINNESOTA—*Ramsey County*: St. Paul, 2 (MINN); *Wabasha County*: Mazeppa, 1 (UM); WISCONSIN—*Iron County*: iron mine at Hurley, 1 (MINN); *Crawford County*: Soldiers Grove, 2 (UW); *Richland County*: Eagle Cave, 10 mi. SW Richland Center, 9 (UI), 4 (UW); John Gray Cave, 2 (UW); *Grant County*: Atkinson's Diggings, 2¼ mi. W Beetown, 14 (UI); Crystal Cave, 1 (UW); Snake Cave, Potosi, 2 (KU); *Iowa County*: Mineral Point, 1 (UW); NEW YORK—*Essex County*: Keene Heights, 1 (MCZ); *Livingstone County*: Portage, 1 (USNM); *Cattaraugus County*: Allegheny State Park, 1 (KU); *Tompkins County*: Ithaca, 11 (CU), 4 (KU), 1 (UI), 1 (NYSM); *Otsego County*: Otsego Lake, Hyde Hall, 1 (NYSM); *Albany County*: Haile's Cave, John B. Thatcher State Park, 2 (UC), 1 (CU), 1 (MCZ); Upper Ward Cave, Clarksville, 18 (AMNH), 1 (WGF), 1 (MCZ); *Orange County*: West Point, 6 (USNM); VERMONT—*Rutland County*: Brandon, 2 (FLO), 1 (MCZ), 4 (USNM); N. Chittenden, 6 (AMNH); Chittenden, 1 (AMNH), 1 (OSM), 1 (FLO); Proctor, 2 (USNM); *Windsor County*: Plymouth Union, 1 (MCZ); *Bennington County*: E. Dorset, 3 (FLO), 2 (USNM); MASSACHUSETTS—*Berkshire County*: Lanesboro, 1 (MCZ); *Worcester County*: E. Templeton, 1 (MCZ); *Middlesex County*: 5 mi. E Ayer, 1 (UI); Concord, 1 (MCZ); *Hampden County*: emery mine, ½ mi. W Chester, 8 (MU), 4 (MCZ); *Norfolk County*: Braintree, 1 (MCZ); *Barnstable County*: Mashpee, 1 (CU); CONNECTICUT—*Litchfield County*: Twin Lakes Cave, Lakeville, 2 (UC); iron mine, Roxbury, 2 (MCZ); *Tolland County*: 2 mi. NW Storrs, 3 (UC); NEBRASKA—*Sarpy County*: limestone quarry, ½ mi. W Meadows, 5 (WGF); *Cass County*: 1½ mi. NE Louisville, 3 (CNHM); ILLINOIS—*Jo Daviess County*: Galena, 1 (UI); lead mine 9 mi. SE Galena, 1 (UI); *Carroll County*: Smith's Cave, 2 mi. W Mt. Carroll, 1 (WGF), 3 (UI); *LaSalle County*: Blackball Mine, 1¾ mi. W Utica, 4 (CNHM), 7 (WGF), 22 (UI); Pruce's Mine, Utica, 1 (UI); *Adams County*: Burton Cave, 14 mi. SE Quincy, 2 (CNHM), 2 (UI); *Jersey County*: cave at Grafton, 1 (UI); *Jasper County*: Sainte Marie, 1 (UI); *Richland County*: Olney, 1 (USNM); *Monroe County*: Eckhart Cave, Burksville, 2 (UC), 19 (UI); *White County*: 2 mi. S and 6 mi. E Crossville, 1 (UI); *Jackson County*: Natural Bridge, Pomona, 1 (UF); sandstone cave in Giant City State Park, ½ mi. E Makanda, 2 (WGF); *Williamson County*: W side Grassy Lake, 1 (UI); *Saline County*: Cave Hill Cave, 8 mi. SE Harrisburg, 13 (UI); *Union County*: Mountain Glen, 3 mi. SW Cobden, 1 (UF); Lickcreek, 2 (USNM); Pine Hills, near Wolf Lake, 1 (UI); Lily Cave, 10 mi. E Anna, 3 (CNHM); *Johnson County*: Ozark, 1 (CNHM); *Pope County*: Golconda, 18 (CNHM); *Hardin County*: 5 mi. W and 1 mi. N Elizabethtown, 2 (UI); Rosiclare, 19 (CNHM); *Alexander County*: mine 3½ mi. NNW Elco, 1 (WGF); abandoned ganister mine, 1 mi. E Elco, 2 (UI); Olive Branch, 7 (CNHM); INDIANA—*Owen County*: cave 6 mi. S

Spencer, 3 (UI); *Monroe County*: Truitts Cave, Bloomington, 1 (UI); Mayfields Cave, Bloomington, 6 (UI), 3 (MCZ), 3 (USNM); Saltpeter Cave, Bloomington, 1 (USNM); Coons Cave, 8 mi. SW Bloomington, 2 (UI), 2 (USNM); Bruckners Cave, 2 (UI); Mothers Cave, 2 (USNM); *Bartholomew County*: Waymanville, 1 (USNM); *Greene County*: Rays Cave, Ridgeport, 7 (UI), 1 (USNM); *Lawrence County*: Mitchell, 1 (CNHM), 1 (UI), 1 (USNM); *Jackson County*: Houston, 1 (USNM); Spraytown, 1 (USNM); Freetown, 1 (USNM); Tampico, 1 (USNM); *Crawford County*: Wyandotte Cave, 5 (UI); Saltpeter Cave, 12 (WGF); Sieberts Well Cave, 1 (CNHM); Wildcat or Sheep Cave, 3 (CNHM); *Harrison County*: cave 1 mi. S Laconia, 1 (UI); *Posey County*: Hovey Lake, 1 (UM); OHIO—*Seneca County*: Goods Cave, Flat Rock, 1 (OSM), 4 (USNM); *Medina County*: 2 (OSM); *Union County*: Marysville, 2 (OSM); *Hocking County*: Bat Cave, Laurel Twp., 1 (KU); *Ross County*: cave at Bainbridge, 2 (USNM); *Clermont County*: E. Fork, Elk Lick, 1 (UC); *Adams County*: Tiffin Twp., 1 (OSM); PENNSYLVANIA—*Warren County*: 1 mi. SE Garland, 1 (CM); *Mercer County*: 2½ mi. SW Mercer, 1 (CM); *Center County*: Penns Cave, Center Hall, 1 (CU); Woodward Cave, 1½ mi. W Woodward, 10 (CM); *Monroe County*: Hartman Cave, 2½ mi. SW Stroudsburg, 1 (CM); *Beaver County*: 1 mi. NE Darlington, 1 (CM); Beaver, 1 (USNM); *Mifflin County*: Aitkin Cave, 1 mi. NE Siglerville, 1 (AMNH), 2 (CU), 1 (MCZ); *Berks County*: 2 mi. E Shoemakerville, 2 (CM); *Cumberland County*: Carlisle, 1 (USNM); *Franklin County*: Needys Cave, 2 (CU); NEW JERSEY—*Warren County*: Pahaquarry Twp., 1 (CU); *Morris County*: Hibernia Mine, Hibernia, 1 (KU); Montville, 1 (CU); Jacksonville, 3 (CU); Brook Valley, 7 (CU); *Union County*: Pepack Cave, 5 (CU); KANSAS—*Marshall County*: gypsum mine, 1½ mi. W and ¼ mi. N Blue Rapids, 11 (KU), 8 (UM); *Leavenworth County*: Leavenworth, 2 (WGF), 2 (KU); 1 mi. SSE Leavenworth, 2 (WGF), 1 (KU); *Butler County*: 6 mi. S El Dorado, 1 (WGF), 5 (KU); *Barber County*: 4 mi. S Sun City, 1 (USNM); Harvard Cave, 4½ mi. S Sun City, 5 (KU); 5 mi. S Sun City, 3 (KU); Dancing Cave, 5½ mi. S Sun City, 1 (KU); ½ mi. N Natural Bridge, 1 (KU); *Cowley County*: 1 mi. W Winfield, 9 (KU); *Cherokee County*: mine tunnel, 1½ mi. S Galena, 1 (WGF), 2 (KU); MISSOURI—*Boone County*: Rocheport Cave, Rocheport, 1 (WGF), 4 (LSU), 13 (UMO); Tumblesons Cave, 8 mi. S Columbia, 3 (UMO); Hunters Cave, 5 (UMO); Devil's Ice Box, 1 (UMO); *St. Louis County*: Eureka, 1 (UMO); *Franklin County*: Merramac State Park, 2 (UMO); Bear Cave, 3 (UMO); *St. Clair County*: Monegaw Springs, 2 (CNHM), 1 (KU); *Camden County*: Ha-fla-tonka River Cave, Camdenton, 6 (CNHM); *Pulaski County*: Piquet Cave, Dixon, 1 (UMO); Bat Cave, 5 mi. S Crocker, 1 (UI), 1 (UMO); Berry Cave, Laquey, 1 (USNM); Berry Cave, 8 mi. S Waynesville, 1 (UI); *Ste. Genevieve County*: 3 (UMO); *Iron County*: cave ½ mi. N Pilot Knob, 2 (KU); *Madison County*: Saltpeter Cave, 1 (UMO); *Texas County*: Chimney Rock Cave, Arrol, 1 (UMO); *Shannon County*: Arrol, 1 (UMO); *Wayne County*: Mill Spring, 2 (CNHM); *McDonald County*: Saltpeter Cave, E of Cyclone, 1 (UMO); cave 3 mi. S Noel, 1 (WGF); *Barry County*: 4 mi. W Exeter, 1 (TNHC); Rock House Cave, 7 mi. E Cassville, 1 (UI); Roaring River State Park, 10 (KU), 2 (UMO); *Stone County*: Old Spanish Cave, 4 mi. N Reeds Spring, 1 (KU); Fairy Cave, 5½ mi. S Reeds Spring, 1 (KU); Mud Cave, 5½ mi. S Reeds Spring, 2 (UI), 1 (KU); Marvel Cave, 1 (UMO); Rockwell Cave, 1 (UMO); KENTUCKY—*Carter County*: Carter Cave, 7 (WGF), 31 (UI), 4 (UM), 1 (OSM), 4 (USNM); Oligonuck Cave, Carter City, 5 (UI); Cascade Cave, 2 (MCZ); *Boyd County*: Catlettsburg, 1 (USNM); *Bullitt County*: Wildcat Canyon, Burnheim Forest, 2 (UI); *Pulaski County*: Cumberland Cave, 6 mi. SE Burnside, 2 (UM); *Edmonson County*: Dixon Cave, 1 (CNHM); Floyd Collins Crystal Cave, 1 (USNM); Colossal Cave, 6 (KU), 1 (USNM); Long Cave, 8 (KU), 2 (USNM); Mammoth Cave, 2 (USNM); *Powell County*: Slade, 1 (UM); WEST VIRGINIA—*Marshall County*: 3 mi. SE Triadelphia, 9 (WGF); *Monongalia County*: 3 mi. NE Morgantown, 1 (WGF); Morgantown, 1 (WGF); 5 mi. S Morgantown, 7 (WGF); Cheat Lake, 2 (WGF); near head of Cheat Lake, 2 (WGF); Lower Beaverhole Cave, 2 (WGF); 1½ mi. ESE Hagans, 5 (WGF); Dellslow Cave, 1 mi. SE Dellslow, 1 (WGF); *Preston County*: Upper Beaverhole Cave, 1 (WGF); Cornwell Cave, 5 mi. E Masontown, 7 (WGF); *Mineral*

County: Ridgeville Cave, 4½ mi. WNW Burlington, 1 (WGF); Saltpeter Cave, 5 mi. SW Burlington, 1 (WGF); *Hampshire County*: 1 (USNM); *Jefferson County*: John Brown's Cave, Harpers Ferry, 3 (UM); Charles Town, 1 (USNM); *Tucker County*: Mill Run Cave, 6 mi. ESE Hendricks, 1 (WGF); Arbegast Cave, 6 mi. SE Hendricks, 2 (WGF); *Grant County*: Kline's Gap Cave, 4 mi. SW Maysville, 1 (WGF); Cabins, 1 (WGF); 3 mi. W Petersburg, 2 (WGF); *Randolph County*: Bazzle Cave, 1 mi. SE Harman, 1 (WGF); *Pendleton County*: Smokehole Cave, 1 (CU); 5½ mi. N Upper Tract, 5 (WGF); Cave Mt. Cave, 4 (WGF); 2 mi. S Mouth of Seneca, 1 (WGF); Schoolhouse Cave, 5½ mi. NE Riverton, 1 (WGF); Franklin, 3 (USNM); Hamilton Cave, 3½ mi. SW Franklin, 2 (WGF); Trout Cave, 3½ mi. SW Franklin, 1 (WGF); 5 mi. SSW Franklin, 1 (WGF); 5 mi. S Franklin, 3 (WGF); Rexroad Cave, 7 mi. SW Franklin, 1 (WGF); Thorn Mt. Cave, 9 mi. S Franklin, 2 (WGF); *Cabell County*: 5 mi. E Huntington, 1 (WGF); 2½ mi. ENE Barboursville, 9 (WGF); *Kanawha County*: 1 mi. S Dunbar, 1 (CU); *Webster County*: 1 mi. W Camden-on-Gauley, 2 (WGF); *Pocohontas County*: Overholt's Blowing Cave, 3 mi. W Marlinton, 1 (WGF); Martha's Cave, 2 mi. WSW Hillsboro, 1 (WGF); *Wayne County*: 4 mi. S Kenova, 1 (WGF); 1½ mi. W Lavalette, 13 (WGF); 1 mi. W Lavalette, 5 (WGF); 2 mi. N Wayne, 2 (WGF); *Lincoln County*: Midkiff, 1 (WGF); abandoned coal mine, ½ mi. E. Midkiff, 3 (WGF); 1 mi. W Ranger, 3 (WGF); *Fayette County*: ½ mi. SE Page, 1 (WGF); *Greenbrier County*: 1½ mi. WSW Frankford, 3 (NCS); Organ Cave, 1 (WGF); *Mingo County*: 3 mi. E Belo, 1 (WGF); *Logan County*: abandoned coal mine, 1 mi. E Chapmanville, 2 (WGF); abandoned coal mine, 2 mi. E Chapmanville, 1 (WGF); *Wyoming County*: 3 mi. W Pineville, 1 (WGF); *Monroe County*: Laurel Creek Cave, 1½ mi. NE Greenville, 10 (UI); Greenville Saltpeter Cave, ½ mi. NE Greenville, 3 (WGF); Patton Cave, Gap Mills, 1 (WGF); Argobrites Cave, 1 (WGF); MARYLAND—*Montgomery County*: Capitol View, 1 (USNM); *Prince George County*: near D.C. line, 4 (USNM); *Charles County*: Marshall Hall, 6 (USNM); *St. Marys County*: St. George Island, 2 (USNM); DELAWARE—*Sussex County*: Seaford, 1 (AMNH); VIRGINIA—*Shenandoah County*: cave near Quicksburg, 2 (CU); *Warren County*: Rogers Cave, 2 (USNM); *Fairfax County*: 1 (USNM); *Rockingham County*: Endless Caverns, 1 (USNM); *Spotsylvania County*: Fredericksburg, 4 (USNM); *Bath County*: Hot Springs Cave, 6 (MCZ), 4 (USNM); *Craig County*: Murder Hole Cave, 2 (USNM); *Giles County*: cave near Newport, 3 (USNM); *Montgomery County*: 1 mi. SE Blacksburg, 4 (UM), 20 (USNM); *Amelia County*: Amelia C. H., 2 (USNM); *Russell County*: Bundy Cave, near Lebanon, 6 (UM); *Norfolk County*: Lake Drummond, Dismal Swamp, 1 (USNM); *Fairfax County*: Potomac River, near mouth of Difficult Run, 4 (USNM); OKLAHOMA—*Ottawa County*: 2 mi. S and 2 mi. E Fairland, 1 (OAM); 11 mi. S and 2 mi. W Wyandotte, 2 (OAM); *Woodward County*: Alabaster Caverns, 1 (OAM); *Delaware County*: Black Hollow Cave, S Spavinow Lake, 1 (OAM); Cochrans Trout Cave, 3 mi. NW Maysville, 1 (OAM); cave 1 mi. W Maysville, 1 (OAM); 2½ mi. N Topsy, 2 (OAM); Duncan Cave, 3 mi. SSE Colcord, 4 (OAM); Stansbury Cave, 1 (OAM); *Tulsa County*: 8 mi. W Red Fork, 2 (USNM); *Cherokee County*: 1 (OAM); Half Moon Cave, ½ mi. NW Gideon, 1 (OAM); Muskogee B. S. Camp, 1 (OAM); Cottonwood Cave, 2 (OAM); *Adair County*: Bat Cave, 4½ mi. SE Kansas, 9 (WGF), 16 (UI), 10 (OAM); Ross Mt. Cave, 7 mi. W Stillwell, 13 (KU); Cave Spring Cave, Lyons, 4 (UI), 3 (OAM); Crystal Cave, near Bunch, 4 (UI), 30 (OAM); Chris Petkoff's Cave, 3 (OAM); *Muskogee County*: Wildlife Conservation Station, Bragg, 1 (OAM); Big Greenleaf Creek, above Greenleaf Lake, 4 (OAM); *Washita County*: 5 mi. S and 5 mi. W Weatherford, 2 (KU), 2 (OAM); *LaFlore County*: Kiamichi Mt. Cave, S of Muse, 3 (OAM); Little River bridge at Honobia, 4 (OAM); *Harmon County*: 3 mi. W and 1 mi. S Reed, 1 (OAM); *Greer County*: 3½ mi. N Jester, 3 (OAM); *Kiowa County*: Windmill Cave, 15 mi. S and 3 mi. W Carnegie, 1 (OAM); *Murray County*: Mystic Cave, 8 mi. S and 1½ mi. E Sulphur, 4 (OAM); *McCurtain County*: Forked Lake, S of Eagletown, 2 (OAM); 4 mi. E and 3 mi. S Tom, 1 (OAM); Red River, 6 mi. S Tom, 2 (TNHC); ARKANSAS—*Benton County*: Treasure Cave, 2 mi. NW Gravette, 2 (MCZ); Crystal Cave, 8 mi. NW Bentonville, 3 (WGF); Logan Cave, 8 mi. ENE Siloam Springs, 10 (UI); *Washington County*: cave near Springdale,

1 (CNHM); Nichols Cave, near Hicks, 1 (UI); Granny Dean Cave, Sulphur City, 5 (CNHM); Devil's Den, Devil's Den State Park, 1 (CNHM), 4 (UI), 29 (KU); *Madison County*: 1 (CU), 1 (WGF); Denny Cave, Alabam, 2 (WGF); Pettigrew, 1 (USNM); *Independence County*: Ferrell Cave, 1 mi. W Cushman, 10 (UI); Cushman Cave, 3 (CNHM); Forshees Cave, 3 (CNHM); Bone Cave, 1 (CNHM); TENNESSEE—*Obion County*: Reelfoot Lake, 1 (USNM); *Scott County*: 5 mi. W Robbins, 1 (OAM); *Anderson County*: Briceville, 2 (USNM); *Cocke County*: Low Gap, 4½ mi. SE Cosby, 2 (USNM); *Blount County*: Gregory Cave, Cades Cove, 1 (UC); *Sevier County*: Gatlinburg, 3 (OSM); *Lewis County*: 9 mi. S Hohenwald, 3 (LSU); *Grundy County*: Wonder Cave, near Monteagle, 5 (UI); Sink Hole Cave, near Wonder Cave, 2 (CNHM); *Hamilton County*: Rathburn, 2 (USNM); *county unknown*: Indian Cave, 1 (MCZ); NORTH CAROLINA—*Wake County*: Raleigh, 1 (CNHM), 1 (NCS), 7 (USNM); *Bertie County*: Sans Souci, 1 (USNM); *Madison County*: Marshall, 1 (MCZ); *McDowell County*: Linville Caverns, 6 (WGF), 1 (UM); *Graham County*: Marble, 1 (UM); *Mecklenburg County*: Charlotte, 2 (NCS); TEXAS—*Shelby County*: Neuville Cave, 10 mi. S Center, 2 (UI); *Walker County*: 11 mi. NW New Waverly, 1 (TNHC); *Polk County*: 4 mi. E Livingston, 2 (TWRC); 3 mi. S Livingston, 1 (TWRC); *Travis County*: 3 mi. W Austin, 1 (TNHC); *Edwards County*: Devils Sink Hole, 8 mi. ENE Rocksprings, 4 (TNHC); *Kerr County*: Bear Creek, 5 mi. W Hunt, 1 (TWRC); Turtle Creek, 8 mi. SW Kerrville, 2 (TWRC); *Kendall County*: 16 mi. NE Boerne, 1 (TNHC); 5 mi. S Boerne, 1 (TNHC); *Comal County*: Brehmmer Cave, 10 mi. W New Braunfels, 4 (UI); *Harris County*: 4 mi. N Huffman, 1 (TWRC); *Bandera County*: 7 mi. SW Medina, 1 (TNHC); *Bexar County*: Dead Mans Cave, 12 mi. E Boerne, 5 (OAM); San Antonio, 1 (CNHM); Kelly Air Force Base, 1 (KU); *Uvalde County*: 6 mi. NW Utopia, 1 (TNHC); *Bee County*: 2 (AMNH); *Cameron County*: Brownsville, 1 (USNM); LOUISIANA—*Lincoln Parish*: Ruston, 1 (LSU); *Natchitoches Parish*: Provencal, 2 (LSU); Vowells Mills, 1 (LSU); *Grant Parish*: Fishville, 1 (LSU); *Washington Parish*: 10 mi. W Bogalusa, 1 (LSU); *East Baton Rouge Parish*: 17 mi. NW campus, 1 (LSU); Baton Rouge, 3 (LSU); 2 mi. S University, 1 (LSU); *St. Tammany Parish*: St. Tammany, 1 (AMNH); *Terrebonne Parish*: Houma, 1 (USNM); MISSISSIPPI—*Tishomingo County*: silica mine, near Eastport, 1 (JSW); *Union County*: near New Albany, 1 (JSW); *Wayne County*: Pitts Cave, 6 mi. NW Waynesville, 15 (LSU); *Hancock County*: Bay St. Louis, 3 (USNM); ALABAMA—*Limestone County*: Salt River Cave, ½ mi. W Goode Springs, 1 (CNHM); Elkmont, 2 (USNM); *Madison County*: Shelta Cave, Huntsville, 2 (UI); *Jackson County*: Stevenson, 1 (USNM); *Colbert County*: 10 mi. N Leighton, 1 (USNM); *Lawrence County*: Saltpeter Cave, 1 (JSW); *Morgan County*: Hughes Cave, 6 mi. E Florette, 21 (UI); *DeKalb County*: Ft. Payne, 2 (USNM); *Pickens County*: S of Gordo, 1 (JSW); *county unknown*: Bucks Pocket, 1 (USNM); GEORGIA—*Gwinnett County*: Roswell, 4 (MCZ); *Fulton County*: Ft. McPherson, 1 (USNM); *Chattahoochee County*: Ft. Benning, 1 (CU); *Liberty County*: 3 mi. SW Riceboro, 2 (UI); *Decatur County*: 12 mi. SW Bainbridge, 1 (UM); *Grady County*: Waterfall Cave, 7 mi. N Cairo, 24 (UI), 1 (USNM); 4 mi. S Beachton, 1 (UI); *county unknown*: cave at West Shoals, 1 (CU); *state only*: 1 (USNM); FLORIDA—*Escambia County*: 4 (FSBH); *Jackson County*: Old Indian Cave, 3 mi. N Marianna, 9 (FSBH), 2 (UF), 12 (WGF); *Gulf County*: Appalachicola River, 18 mi. above mouth, 1 (USNM); TAMAULIPAS—near headwaters Rio Sabinas, 8 km. W and 10 km. N El Encino, 2 (KU); Rancho Pano Ayuctle, 6 mi. N Gomez Farias, 1 (KU).

Additional records.—ONTARIO—*Carlton County*: Ottawa (Anderson, 1946); *Hastings County*: cave near Latta (*ibid.*); *Addington County*: Puzzle Lake Cave (*ibid.*); *Wellington South County*: Rockwood (*ibid.*); *Halton County*: Bronte (*ibid.*); *Lincoln County*: Niagara-on-the-Lake (*ibid.*); QUEBEC—*Joliette County*: Joliette (*ibid.*); MINNESOTA—*Sterns County*: St. Cloud (Goehring, 1954); *Hennepin County* (Gunderson and Beer, 1953); *Scott County* (*ibid.*); *Nicollet County*: St. Peter (Swanson and Evans, 1936); WISCONSIN—*Sauk County*: Devil's Lake, in the Baraboo Range (Jackson, 1919); MAINE—*state only* (Hall and Dalquest, 1950); IOWA—*Dubuque County*: Dubuque (Scott, 1939); *Jackson County*: Maquoketa,

Maquoketa State Park (*ibid.*); ILLINOIS—*Champaign County*: Urbana (Necker and Hatfield, 1941); INDIANA—*Tippecanoe County*: Purdue Dairy Woods, W. Lafayette (Mumford, *in litt.*); *Parke County*: Sugar Creek, Turkey Run State Park (*ibid.*); OHIO—*Sandusky County*: Freemont (Bole and Molethrop, 1942).

Pipistrellus subflavus clarus Baker

Pipistrellus subflavus clarus Baker, Univ. Kans. Publ., Mus. Nat. Hist., 7 (10): 585, November 15, 1954.

Type locality.—Two mi. W Jiménez, elev. 850 ft., Coahuila, Mexico.

Range.—Northern Coahuila and adjacent parts of Texas (see map, Fig. 2).

Diagnosis.—A race of *Pipistrellus subflavus* characterized by pale color. Color varies from pale yellow to yellow-orange. Size large.

Comparisons.—Since the range of this race borders upon only that of *P. s. subflavus*, it needs comparison with that form only. Compared with a series from Carter Cave, Carter County, Kentucky, *P. s. clarus* differs in being paler and slightly larger. It is also paler than specimens from the region of the Edwards Plateau of Texas.

Remarks.—In Baker's diagnosis and comparisons, he intimates that the zygomata are more expanded laterally in *P. s. clarus* than in *P. s. subflavus*. The present study has failed to indicate such a difference.

It is interesting to note that *P. s. clarus* is separable from the pipistrels inhabiting the Edwards Plateau of Texas. Here, pipistrels occur rather sparingly in the caves in winter and also as summer residents along the streams of the region. Most of the region between the ranges of the two forms, including much of the Rio Grande Valley, is uninhabitable for pipistrels. There seems to be a fairly effective ecological barrier between the two races.

Measurements.—Average measurements of five adult females from the type locality are: total length, 86; length of tail, 39; length of foot, 9.8; length of ear, 12.4; length of tibia, 14.1; length of forearm, 33.7; length of third metacarpal, 31.6; length of fifth metacarpal, 30.8; greatest length of skull, 13.1; zygomatic breadth, 8.0; breadth of cranium, 6.7; height of skull, 5.9; and alveolar length of maxillary toothrow, 4.2.

Specimens examined.—Total number 19, from the following localities: TEXAS—*Val Verde County*: Comstock, 1 (USNM); Del Rio, 2 (USNM); COAHUILA—2 mi. W Jiménez, 14 (KU); 2 mi. S and 3 mi. E San Juan de Sabinas, 2 (KU).

Pipistrellus subflavus floridanus Davis

Pipistrellus subflavus floridanus Davis, Proc. Biol. Soc. Wash., 70: 213, December 31, 1957.

Type locality.—Homosassa Springs, at head of Homosassa River, Citrus County, Florida.

Range.—Peninsular Florida and southeastern Georgia. Known from as far south as Bassenger, Okeechobee County, Fla., and ranging northward at least to 5 miles west of Ludowici, Long County, Ga. (see map, Fig. 2).

Diagnosis.—A race of *Pipistrellus subflavus* characterized by complete absence of reddish tones to the fur. Color varies from a pale yellow to chocolate brown and silvery-gray. Base of hair brown or black; subterminal band yellowish or gray; terminal band chocolate brown or black; tips of guard hairs silvery. Size large.

Comparisons.—Since the range of this race borders upon only that of *P. s. subflavus*, it needs comparison with that form only. As compared with a series of 24 specimens taken from Waterfall Cave, 7 miles north of Cairo, Grady County, Ga., on February 5, 1955, *P. s. floridanus* differs markedly in color. The basal region of the hair is similar in the two races. The subterminal band in *P. s. subflavus* is a light orange or reddish in color, whereas in *P. s. floridanus* it is white to a pale yellow, and lacking entirely in reddish hues. The terminal band is a dark reddish brown in *P. s. subflavus*; in *P. s. floridanus* this band ranges from brown to black

in color. The tips of the guard hairs of *P. s. subflavus* are orange in color in contrast to the pale yellow or silver of *P. s. floridanus*.

In size, *P. s. floridanus* does not differ from specimens of *P. s. subflavus* from the Atlantic seaboard, but is slightly larger than those from the Ohio River Valley. Compared with large series from the vicinity of Huntington, W. Va., Carter Cave, Ky., Rosiclare, Ill., and Adair County Bat Cave, Okla., *P. s. floridanus* is slightly larger in all measurements except length of the toothrow. It is not larger than the average of a large series from Washington, D.C.

Measurements.—Average measurements of three adult males from the type locality are: total length, 86; length of tail, 39; length of foot, 9.7; length of ear, 13.0; length of tibia, 13.0; length of forearm, 33.0; length of third metacarpal, 31.7; length of fifth metacarpal, 30.5; greatest length of skull, 13.1; zygomatic breadth, 7.9; breadth of cranium, 6.6; height of skull, 6.0; and alveolar length of maxillary toothrow, 4.1.

Specimens examined.—Total number 153, from the following localities: GEORGIA—*Long County*: 5 mi. W Ludowici, 1 (UG); *county unknown*: Okefenokee Swamp, Billy's Island, 5 (CU); Okefenokee Swamp, Chesser's Island, 1 (CU); FLORIDA—*Hamilton County*: 1 (FSBH); *Columbia County*: 4 (FSBH); *Baker County*: 1 (FSBH); *Taylor County*: 6 (FSBH); *Bradford County*: 1 (FSBH); *Clay County*: 6 (FSBH); *Dixie County*: 2 (FSBH); *Gilchrist County*: 1 (FSBH); *Alachua County*: 30 (FSBH); 2 mi. E Gainesville, 1 (UC); 5 mi. E Gainesville, 5 (HBS), 3 (UF); 6 mi. E Gainesville, 1 (UM); *Putnam County*: 6 (FSBH); *Levy County*: 9 (FSBH); Gulf Hammock, 1 (UF); Waccasassa River, 2 mi. N Gulf Hammock, 2 (AMNH); *Marion County*: 20 (FSBH); Blitche's Ferry, 10 mi. E Ocala, 2 (MCZ); *Citrus County*: 1 (FSBH); Homosassa Springs, at head of Homosassa River, 3 (AMNH); *Sumter County*: 36 (FSBH); *Orange County*: 1 (FSBH); Lake Underhill,

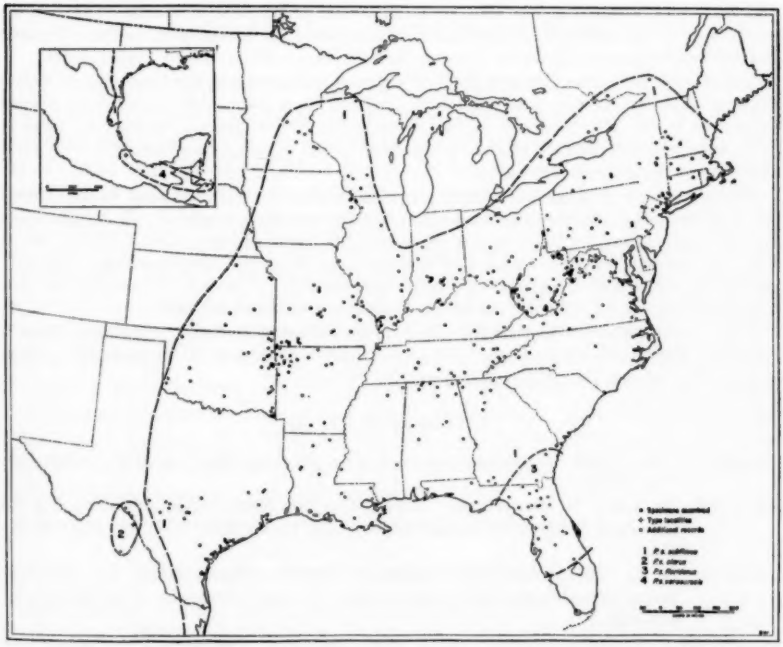

FIG. 2.—Geographical ranges of the subspecies of *Pipistrellus subflavus*.

Orlando, 1 (USNM); *Pasco County*: 1 (FSBH); *Polk County*: Winterhaven, 1 (UF); *Okeechobee County*: Bassenger, 1 (AMNH).

Additional record.—FLORIDA—*Pinellas County*: Tarpon Springs (Sherman, 1936).

Pipistrellus subflavus veraecrucis (Ward)

Vesperugo veraecrucis Ward, Amer. Nat., 25: 745, August, 1891.
Pipistrellus veraecrucis Miller, N. Amer. Fauna 13: 93, October 16, 1897.
Pipistrellus subflavus veracrucis [*sic*] Hall and Dalquest, Univ. Kans. Publ., Mus. Nat. Hist., 1 (26): 601, January 20, 1950.

Type locality.—A cave "Close by the hamlet of Las Vigas," Canton of Jalapa, Veracruz, Mexico.

Range.—Eastern Mexico and Honduras. Limits of range unknown.

Diagnosis.—A race of *Pipistrellus subflavus* characterized by small size, both of body and cranial measurements, and dark color. Color varies from a deep reddish brown to dark brown, on both dorsal and ventral surfaces.

Comparisons.—Compared with all other races of *P. subflavus*, *P. s. veraecrucis* is decidedly smaller, particularly in cranial measurements. The color is generally darker than that of *P. s. subflavus*, although some individuals are indistinguishable in this regard from certain specimens from Alabama and other parts of the range of this race.

Remarks.—This race apparently inhabits the tropical lowlands of eastern Mexico, as well as the mountainous region of the type locality. One specimen (KU) was taken at 300 feet elevation, 30 km. SSE of Jesús Carranza. In view of this, it is surprising that three specimens from the tropics of southern Tamaulipas (Rancho Pano Ayuctle, 6 mi. N of Gomez Farias, 300 feet; and near the headwaters of Rio Sabinas, 8 km. W and 10 km. N of El Encino, 400 feet) are much closer to typical *P. s. subflavus* than to *P. s. veraecrucis*. Ecologically, southern Tamaulipas seems to have more affinity to Veracruz than to Texas and the eastern United States.

It is of interest to note that both the type series and the series at the University of Kansas Museum of Natural History from 4 km. E of Las Vigas were taken while hibernating, whereas those from coastal Honduras and the one from 30 km. SSE of Jesús Carranza were taken in May. It may be that this race inhabits the lowland tropics in summer and moves into the caves and mines in the mountains in winter.

Measurements.—Average measurements of eight adult males and four adult females from 4 km. E of Las Vigas, 8500 feet, Veracruz, are, respectively: total length, 77, 83; length of tail, 34, 36; length of foot, 7.3, 7.6; length of ear, 13.0, 13.8; length of forearm, 31.4, 31.9; length of third metacarpal, 29.7, 29.8; length of fifth metacarpal, 28.1, 28.3; length of tibia, 13.1, 13.8; greatest length of skull, 12.4, 12.6; zygomatic breadth, 7.3, 7.5; breadth of cranium, 6.3, 6.4; height of skull, 5.7, 5.7; and alveolar length of maxillary toothrow, 3.9, 4.0.

Specimens examined.—Total number 18, from the following localities: VERACRUZ—4 km. E Las Vigas, 8500 ft., 14 (KU); 30 km. SSE Jesús Carranza, 300 ft., 1 (KU); HONDURAS—Jilimo Farms, Tela District, United Fruit Company, 3 (UM).

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A NEW PIPISTREL FROM OKLAHOMA AND TEXAS

BY BRYAN P. GLASS AND RICHARD C. MORSE

A hitherto unrecognized race of *Pipistrellus hesperus* has recently been discovered in the Wichita Mountains of Oklahoma and along the cap rock at the eastern border of the Llano Estacado in Texas. The species *P. hesperus* has not previously been reported from Oklahoma or any locality east of the Pecos River in New Mexico and Texas (Hall and Dalquest, 1950). According to these authors there are no published records to indicate that the range of the eastern pipistrel, *P. subflavus*, at any point overlaps that of *P. hesperus*, although the ranges of the two virtually meet in the vicinity of Del Rio, Texas. The range extension reported herein extends the known range of *P. hesperus* some 75 miles east of the western limit of range for *P. subflavus* (Glass, 1955). Apparently there is little actual competition between the two species, for the former is saxicolous while the latter is cavernicolous, and is also quite rare throughout the region of overlap.

Acknowledgments are due to Donald F. Hoffmeister, University of Illinois; Miss Viola S. Schantz, U.S. Fish and Wildlife Service; Paul F. Spangle, Carlsbad Caverns National Park; and Russell W. Strandtmann, Texas Technological College, for the loan of specimens used in this study.

The new race of *Pipistrellus hesperus* may be known as:

Pipistrellus hesperus oklahomae subsp. nov.

Type.—Adult female (skin and skull), Oklahoma State University Museum of Zoology No. 2863; from the north side of Granite Mountain, Granite, Greer County, Oklahoma; collected by Bryan P. Glass, June 2, 1955; original No. 1634.

(The type has been sent to the U.S. National Museum for deposit in the Biological Surveys Collection.)

Distribution.—Known from Greer, Kiowa and Comanche Counties, Oklahoma, in the granitic Wichita Mountains, and from near Justiceburg, Garza County, Texas.

Diagnosis.—Size large for the species; females slightly larger than males. Total body length averaging 73.8 in males, 79.6 in females; length of forearm averaging 30.4 in males, 31.2 in females. Skull with length of maxillary tooth row averaging 4.24 in males, 4.30 in females; condylobasal length averaging 12.08 in males, 12.44 in females. Color reddish-brown, brighter on head, lighter beneath.

Measurements (in mm.).—Type: total length, 83; tail, 32; hind foot, 7; ear from notch, 13; tragus, 7; forearm, 32.8; total length of skull, 12.8; condylobasal length, 12.52; maxillary tooth row, 4.21; zygomatic breadth, 8.21; interorbital constriction, 3.5; maxillary breadth at M^3, 5.56; mastoid breadth, 6.82; mandibular tooth row, 4.7.

Average and extreme cranial measurements for five males from Greer and Kiowa counties are: total length of skull, 12.74 (12.6–12.93); condylobasal length, 12.08 (11.79–12.45); maxillary tooth row, 4.24 (4.07–4.48); zygomatic breadth, 8.06 (7.96–8.15); interorbital constriction, 3.56 (3.43–3.65); maxillary breadth at M^3, 5.33 (5.14–5.5); mastoid breadth, 6.72 (6.6–6.8); mandibular tooth row, 4.41 (4.3–4.49). Similar measurements for nine females from Greer and Comanche counties are: total length of skull, 12.79 (12.5–12.95); condylobasal length, 12.44 (12.29–12.52); maxillary tooth row, 4.3 (4.19–4.44); zygomatic breadth, 8.38 (8.21–8.5); interorbital constriction, 3.66 (3.39–3.81); maxillary breadth at M^3, 5.47 (5.3–5.61); mastoid breadth, 6.84 (6.79–6.96); mandibular tooth row, 4.6 (4.46–4.71).

Color.—(Terms in capitals are from Ridgway.) Dorsum between Tawny-Olive and Isabella Color; venter near Cinnamon-Buff; head in region between ears Honey Yellow; hairs on body distinctly bicolor, intense black basally; membranes Blackish Brown. *Young*: dorsum Buffy Olive; venter Sudan—slightly lighter than dorsum; head sometimes slightly brighter than dorsum; hairs on body have poor line of demarcation between root and tip regions, basal half dull Black; membranes Blackish Brown.

Comparisons.—The new form *P. h. oklahomae* has been compared directly with all named forms of the species except *P. h. potosinus* Dalquest. The latter was described by Dalquest (1951) as having dull brown pelage, with average measurements for males and females, respectively, as follows: total length, 74, 80; condylobasal length, 12.2, 12.3; length of maxillary tooth row, 5.1, 5.2. Although the total and condylobasal lengths of *oklahomae* resemble those of *potosinus*, in the maxillary tooth row, the former measures considerably less (4.24, 4.3 in males and females, respectively). The form *oklahomae* has reddish-brown pelage comparable to darker specimens of *Myotis subulatus melanorhinus* from New Mexico and Arizona. When compared to subspecies from other parts

of the United States, *oklahomae* was found most closely to resemble *P. h. maximus* and *P. h. santarosae* in size. Because of very obvious discrepancies in size and color, the forms *P. h. hesperus*, *P. h. australis* and *P. h. merriami* were not investigated further.

The Oklahoma population of this species is best differentiated from its nearest related forms to the west, *P. h. maximus* and *P. h. santarosae*, on the basis of color. Compared to them the new form is much darker, without the buff or gray tones that characterize both of its near neighbors. The brownish wash to be seen on *santarosae* does not compare in shade with *oklahomae*, being much paler. The former is described by Hall and Dalquest (1950) as being between Buffy Brown and Wood Brown.

Remarks.—The specimens from Justiceburg, Texas, came to hand after the collections from Oklahoma had already been compared with the other subspecies. In both measurements and color they agree with the specimens from the Wichita Mountains. The subspecies is therefore likely to be encountered at many points about the cap rock that forms the eastern escarpment of the Llano Estacado. At all points this escarpment is approximately 250 miles from the Pecos River valley in New Mexico where *P. h. maximus* has been reported from near Carlsbad, and *P. h. santarosae* from Santa Rosa. It seems, therefore, that the high plains of the Llano Estacado are the barrier that separates *P. h. oklahomae* from its nearest related forms in New Mexico.

Specimens examined.—Abbreviations used are as follows: Oklahoma State University, OSU; Texas Technological College, TTC; Biological Surveys Collection, USNM; Carlsbad Caverns National Park, CCNP; Illinois University Museum of Natural History, IMNH. *Pipistrellus hesperus oklahomae*: OKLAHOMA—*Comanche County*: Easter Pageant Grounds, Wichita Mountains, 1 (OSU); West Cache Creek at southern boundary of refuge, 1 (OSU). *Greer County*: Custer Cave near monument works at Granite, 2 (OSU); Quarry pond near monument works at Granite, 4 (OSU); west boundary of Quartz Mountain State Park, 1 (OSU); south boundary of Quartz Mountain State Park, 1 (OSU); north side of Granite Mountain, 1 mi. N of Granite (type locality), 20 (OSU). *Kiowa County*: north side of Radziminski Mountain near Mountain Park, 4 (OSU); Svoboda Pond, south side of Radziminski Mountain, 9 (OSU). TEXAS—*Garza County*: near Justiceburg, 4 (TTC). *Pipistrellus hesperus santarosae*: COLORADO—*Montezuma County*: Ashabaugh's Ranch, 1 (USNM). NEW MEXICO: *Eddy County*: Walnut Canyon, 1 (CCNP). *Guadalupe County*: Santa Rosa, 3 (USNM). *Valencia County*: Laguna, 2 (USNM). *Sandoval County*: Jamez, 1 (USNM). *Pipistrellus hesperus maximus*: ARIZONA—*Cochise County*: Carr Canyon, 1 (IMNH); Golden Canyon, 1 (IMNH); Miller Canyon, 6 (IMNH); mouth of Brown Canyon, 1 (IMNH); South Fork Canyon near Portal, 2 (OSU). NEW MEXICO—*Eddy County*: Carlsbad Cave, 2 (USNM); Walnut Canyon, 2 (CCNP). *Hildago County*: Animas Valley, 1 (USNM); Dog Spring, 5 (USNM); Guadalupe Canyon, 3 (USNM). *Luna County*: Florida Mountains, 1 (USNM). TEXAS—*Brewster County*: Alpine, 1 (USNM); Boquillas, 1 (USNM); Marathon, 3 (USNM). *Jefferson Davis County*: Davis Mountains, 4 (USNM). *Pipistrellus hesperus australis*: ARIZONA—*Graham County*: 1 mi. E of Fort Grant, 3 (IMNH); Lebanon Reservoir No. 2, 3 (IMNH); Marijilda Camp Ground, 1 (IMNH). *Pipistrellus hesperus hesperus*: ARIZONA—*Coconino County*: Route 64, SE boundary Grand Canyon National Park, 1 (IMNH); SE boundary Grand Canyon National Park, 4 (IMNH). *Yavapai County*: Camp Verde, 2 (IMNH); 1 mi. W of Camp Verde, 2 (IMNH). *Yuma County*: 15 mi. S and 9 mi. W of Hope, 4 (IMNH); 4 mi. W of Yuma, 2 (IMNH).

Pipistrellus hesperus merriami: CALIFORNIA—*San Diego County*: Agua Caliente Spring, 2 (OSU).

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Dept. of Zoology, Oklahoma State Univ., Stillwater. Received December 8, 1958.

A PLEISTOCENE VAMPIRE BAT FROM FLORIDA

BY H. JAMES GUT

The vampire bats, family Desmodontidae, are presently confined to tropical America, ranging northward into Mexico. Fossils appear to be unknown, except for incidental mention by Cushing (1945) of a "vampire bat" in a paper on rodents from San Josecito Cave, in the state of Nuevo Leon, Mexico, and by Cockerell (1930) in a paper describing a new mollusk. More recently Koopman (1958) figured a palate of *Desmodus* from a cave deposit in Cuba.

Recent work in Pleistocene deposits of Florida has disclosed a large number of specimens of a vampire bat related to the living *Desmodus rotundus*. This species is described below.

Desmodus magnus, sp. nov.
(Plate I)

Holotype.—Left dentary with $\overline{C}$, P_3, M_1, Florida Geological Survey No. V–5935. From Bed 2, Illinoian stage of Pleistocene, at Dixie Lime Products Company mine, 1 mi. SE of Reddick, Marion County, Florida, in SW corner, NW ¼, Sec. 14, T. 13 S, R. 21 E. Collected by H. James Gut, September 13, 1953, original No. 2089.

Paratypes.—Eight dentaries, H. James Gut Nos. 2082, 2087, 2089 (right), 2090, 2091, 2093 and 2097.

Diagnosis.—Similar to living *Desmodus rotundus rotundus* (Geoffroy) of South America and *D. r. murinus* Wagner of Mexico and Central America, but mandible longer and teeth wider (Table 1).

Referred material.—Incomplete right maxilla with C, P^4, M^1 (2088). Also 13 clavicles (2078), 21 humeri (2075), 2 radii (2095), $\overline{7}$ femora (2077), 3 tibiae (2079), all complete, from the type locality. Complete humerus (2048) from Illinoian stage of Pleistocene, at Haile, Alachua County, Florida (for location of

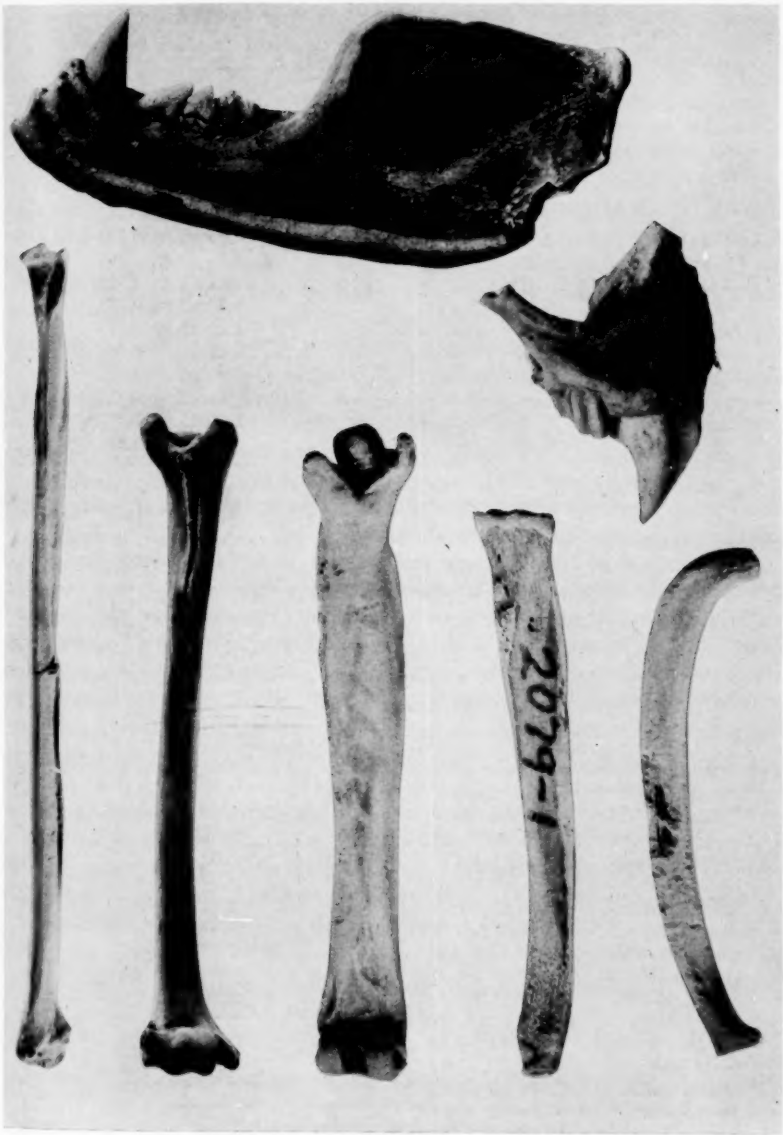

PLATE I

Desmodus magnus sp. nov. Holotype mandible (× 5) and referred maxillary (× 5), radius (× 2), humerus (× 2), femur (× 4), tibia (× 4) and clavicle (× 4). Photographs by Robert D. Weigel.

TABLE 1.—*Jaw and tooth measurement of Desmodus in mm.*

MEASUREMENT	*D. magnus*	NO.	*D. rotundus*	NO.
Mandible length	17.29 (17.27–17.32)	2	15.39 (14.60–16.64)	11
Coronoid height	6.67 (6.6–6.7)	3	6.00 (5.3–6.6)	12
Width behind M_1	0.94 (0.75–1.05)	7	0.84 (0.68–0.98)	12
Length tooth row	3.64 (3.56–3.68)	9	3.47 (3.23–3.68)	12
I_1: Length	0.76 (0.68–0.83)	2	0.77 (0.71–0.83)	12
Width	0.49 (0.45–0.53)	2	0.44 (0.41–0.45)	13
I_2: Length	0.79 (0.79–0.79)	2	0.69 (0.60–0.79)	12
Width	0.45 (0.45–0.45)	2	0.40 (0.38–0.45)	11
$\overline{C}$: Length	1.41 (1.35–1.50)	5	1.33 (1.28–1.42)	11
Width	0.87 (0.75–0.94)	7	0.67 (0.53–0.75)	11
P_2: Length	1.36 (1.28–1.43)	6	1.20 (0.98–1.31)	11
Width	0.53 (0.43–0.56)	7	0.44 (0.38–0.56)	11
P_4: Length	0.97 (0.94–1.05)	8	0.90 (0.79–1.01)	11
Width	0.46 (0.38–0.53)	8	0.41 (0.38–0.45)	11
M_1: Length	1.16 (1.05–1.35)	9	1.21 (1.05–1.35)	11
Width	0.43 (0.38–0.45)	9	0.33 (0.30–0.38)	11

this site see Brodkorb, 1953). In addition, a large number of fragmentary limb elements are at hand from the type locality.

Measurements of limb elements are given in Table 2. Humerus longer and stouter than in either race of *D. rotundus*. Radius longer than in *D. r. murinus*, slightly longer than in *D. r. rotundus*, but stouter than in either modern race. Femur slightly longer than that of *D. r. murinus*, shorter than in *D. r. rotundus*, but stouter than in either modern race. Tibia shorter than in *D. r. rotundus*, equal in length to that of *D. r. murinus*, but stouter than in either of those forms.

TABLE 2.—*Limb measurements of Desmodus in mm.*

MEASUREMENT	*D. magnus*	NO.	*D. rotundus*	NO.
Humerus: Length	41.14 (38.5–43.5)	21	36.46 (33.8–41.3)	7
Proximal width	6.43 (6.1–6.9)	46	4.94 (4.3–5.7)	7
Distal width	6.69 (6.3–7.3)	66	5.37 (5.0–6.3)	7
Medial width	2.67 (2.4–2.9)	49	2.24 (1.9–2.6)	7
Radius: Length	62.46 (58.8–65.7)	3	57.47 (52.7–65.4)	7
Proximal width	4.62 (4.2–4.9)	45	3.70 (3.4–4.2)	7
Distal width	4.48 (4.1–5.2)	28	3.98 (3.5–4.4)	6
Medial width	2.87 (2.5–3.1)	17	2.39 (2.0–2.6)	7
Femur: Length	24.47 (23.6–25.5)	7	23.58 (21.7–26.2)	6
Proximal width	4.57 (4.3–4.8)	12	3.72 (3.5–4.3)	6
Distal width	3.71 (3.5–3.9)	11	3.23 (3.0–3.7)	6
Medial width	3.44 (3.2–3.7)	8	2.38 (2.2–2.9)	6
Tibia: Length	23.20 (22.3–24.3)	3	23.72 (21.8–26.3)	6
Proximal width	3.37 (3.3–3.5)	4	2.85 (2.5–3.2)	6
Distal width	1.95 (1.8–2.0)	4	1.63 (1.4–2.1)	6
Medial width	2.56 (2.4–2.8)	3	1.87 (1.8–2.1)	6
Clavicle length	18.49 (17.3–19.6)	13	16.55 (15.9–17.2)	2

The over-all picture of the fossil vampire is that it was a bat only slightly larger than the living *D. rotundus*, but with stronger teeth and limb bones. The robustness of the fossil vampire is paralleled in some of the other extinct species of vertebrates which have been described from Reddick, several of which are larger or more robust than their living relatives.

Stratigraphy and associated fauna.—The stratigraphy of the Reddick deposit was described by Brodkorb (1957). The bone bed is part of a former cave, now collapsed. It is thought to represent the Illinoian glacial stage of the Pleistocene, since it underlies the Wicomico marine terrace of the Sangamon interglacial stage.

Since its discovery in 1937 by E. J. Moughton, Jr., extensive collecting has demonstrated that the Reddick deposit has one of the richest vertebrate faunas in the world, both as regards species and individuals. A preliminary list of the mammals included 19 species (Gut, 1939), but additional material at hand will bring the mammalian list in the neighborhood of 50 species. The avifauna was studied by Brodkorb (1952, 1957), who determined 52 species of birds. The five reptiles (Auffenberg, 1955, 1956, 1958) and one salamander (Goin and Auffenberg, 1955) hitherto reported represent only a fraction of the herpetofauna of Reddick.

The two localities from which the extinct bat is known both represent the Illinoian stage of the Pleistocene, whereas none of the numerous vertebrate localities from later stages of the Pleistocene is known to contain *Desmodus*.

The Cuban palate reported by Koopman was found in association with other extinct vertebrates. It is said to be larger than the palate of *D. r. murinus* and may well represent the species herein described.

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Modern *Desmodus* material was kindly loaned by Dr. H. B. Sherman and by the authorities of the Chicago Natural History Museum, University of Florida, University of Kansas, Museum of Comparative Zoology, and U.S. National Museum.

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SEXUAL DIMORPHISM IN TEETH OF THE FREE-TAILED BAT

BY CLYDE F. HERREID II

During a recent ecological study of the guano bat, *Tadarida braziliensis mexicana* (Saussure), in Texas, it was necessary to examine many jaws of the animals. As our investigation progressed, we felt that there was some difference in the shape of the upper canines of the male and female, those of the male often appearing concave when viewed from an anterior aspect. To demonstrate this sexual dimorphism satisfactorily, a number of measurements were made of the upper canines.

Bats obtained from Davis Cave, Blanco County, Texas on October 18, November 1 and 15, 1957 were used, all measurements being taken on freshly killed specimens. Most of the bats were held in captivity for some time prior to measuring; some, however, were killed and kept in a cold box until needed. To determine original measurements, only those adult bats whose upper canines showed no wear were used, since any wear would of course influence the length.

Before actual measurements were begun a working technique was established. In place of the glass on the stage of a dissecting microscope a thin sliding tin plate was attached. Room was left between the plate and the rear of the stage for a bat to be passed through. When a bat was to be examined, its upper lip was cut away to facilitate measuring. The head was then placed between the plate and stage with the ventral side of the body facing away from the observer. By tilting the head back and opening the mouth, the canines were directed towards the plate which was inserted between the upper canines and premolars, the bat being hung by his teeth. To maintain it comparatively immobile in this position required moving the plate toward the back of the stage until the head rested firmly between. All measurements were taken with a microcaliper with a vernier scale, and estimations were made to the nearest 0.1 mm.

To determine the number of times it would be necessary to repeat a given measurement (e.g., length of canine) for adequate precision, preliminary tests were made with ten females and ten males. Each of these was examined ten times. Since five distances were being checked, a total of fifty measurements were taken per bat. These examinations were made independently, extending over a number of days. By inspection of the data it was determined to take a minimum of four measurements for each distance. If there was any question about the value, more measurements were taken. Also, because of the small variation occurring in these test replications, it was decided to do each replication consecutively at one session. The standard errors for the twenty trial bats at four replications for length, width, tip, mid-point and base distances were all less than .02 mm. Since no difference occurred in the size of error between males and females, the standard errors were obtained by computing the sum of the squared deviations for each bat's four replications and then pooling them in order to determine the above S.E. values.

Because the variations in the replications were so small and so little difference occurred between the mean and modal values, the mode, the most frequently occurring replication, was selected as the representative figure for the distance for ease of calculation.

Following are specific definitions of the measurements made of the upper canine: (1) *Tip distance*—The anterior outside distance between the tips of the two canines. (2) *Mid-point distance*—The anterior outside distance between the estimated mid-points of the two canines. (3) *Base distance*—The anterior outside distance between the upper canines immediately above the cingula. (4) *Basal width*—The anterior width of either the right or left upper canine immediately above the cingula; no significant difference was noted between the basal width of the right and left canine on the same bat. (5) *Length*—The anterior length of either the right or left upper canine from the cingulum to the tip; this measurement was the only one of the five that needed the aid of the ocular on the dissecting microscope.

During this study a total of 400 bats were examined, 200 of each sex. To help eliminate any daily variation in measurement techniques, both males and females were checked during the same session.

Results and discussion.—Upon examination of the data (Table 1) it is immediately apparent that the male *T. b. mexicana* has a larger upper canine

TABLE 1.—*Upper canine measurements (in mm.) of 400 free-tailed bats*

MEASUREMENT	FEMALE MEAN	MALE MEAN	FEMALE S.D.	MALE S.D.
Tip distance	3.46	3.80	.14	.18
Mid-point distance	3.62	3.78	.13	.15
Base distance	3.80	3.95	.12	.14
Anterior length	1.66	1.88	.10	.11
Basal width	.88	.98	.06	.02

TABLE 2.—*Probabilities that a bat with an upper canine of certain measurements is either male or female*

MEASUREMENT, MM.	FEMALE	MALE	NO. OF BATS
Length classes:			
1.6 or less	.96	.04	111
1.7	.71	.29	89
1.8	.64	.36	63
1.9 or more	.06	.94	137
Width classes:			
.8 or less	.94	.06	68
.9	.75	.25	148
1.0	.14	.86	177
1.1 or more	0.00	1.00	7

than the female. This corresponds with Schwartz's view (Jour. Mamm., 36: 106–109; 1955) that the males generally seem to have a larger skull than do the females. All of these differences are significant at the .01 level.

The tendency for lateral concavity in the male is demonstrated clearly if we look at the mean measurements of the tip, mid-point, and base distances. Note that in both male and female the distance progressively decreases from base to tip. That is, the canines get closer together as they extend further away from the skull. But there is a decided difference in the form of the tooth between the sexes. In the female, the mean decrease from base to mid-point was 0.18 mm. and from mid-point to tip 0.16 mm., while in the males the decrease was 0.16 mm. and 0.03 mm. Thus we see that the female upper canines get closer together at about the same rate from base to mid-point as from mid-point to the tip. In the male the teeth come closer together from the base to the mid-point but very little change occurs from the mid-point to the tip. The difference in the male's 0.03 mm. decrease and the female's 0.16 mm. decrease is significant at the .01 level. The tendency for this lateral flaring-out of the male canine is further emphasized by noting that in 65 per cent of the males no decrease occurred from the mid-point to the tip (22.5 per cent having an actual increase). In contrast, only 5 per cent of the females had no decrease from mid-point to tip (none of them having an increase).

For separating male and female skulls, the length and basal width of the canine are the most effective of the five measurements. In Table 2 I have estimated the probabilities (in terms of these 400 bats) that a bat with a particular upper canine measurement is a male or a female. In the basal width as well as the length there are only two points where the female and male curves overlap significantly, while in the other three measurements there are three points where the sex is indeterminable. Therefore, in attempting to determine sex by these upper characters, we must choose either the width or the length. If, however, there is any wear on these canines, then the length measurement (also tip and mid-point if enough wear is present) are of little

use. The basal anterior width, then, is the most reliable of the five measurements for determining the sex of a bat.

Sexing an unknown group of bats by this method, we take their measurements and compare them with Table 2 to obtain an estimate of the number of each sex. For example, if 1000 skulls had canine width measurements of 0.9 mm., we note the probability under this class as being 0.75 (for a female) and conclude that 750 of these bats were females. Standard errors for these probabilities may be computed.

Since these measurements were all taken on freshly killed specimens, the question of the technique's reliability for "sexing" dry skulls may be asked. Only a small number of dry skulls of known sex have been tested and all fell into the expected groups. It is believed that there is no difference between the tested measurements made on a fresh specimen and those made on a dry skull. Thus, this technique along with other characters of the skull may prove valuable for estimating sex ratios of dead bats in caves. If we can assume no differential mortality between males and females in the caves, then by collecting skulls and "sexing" them we can approximate the sex ratio present in years past. Perhaps, if discernible strata occur in the guano deposits, actual yearly sex ratios can be established for these previous populations. However, care must be taken not to include baby skulls in the sample, since a baby male will probably fall into a female classification. This situation would be most likely to occur in the large nursery caves used by this species.

ACKNOWLEDGMENTS

This investigation was supported by a grant from the National Institutes of Health under the direction of Dr. David E. Davis. Many helpful suggestions were given by Dr. Richard B. Davis during the course of this work.

SUMMARY

The upper canines of 400 free-tailed bats were measured with a microcaliper, five distances being recorded. The canines of males were decidedly larger in all respects. Also, they often were concave in appearance when viewed from the anterior aspect. This was not true for females. A probability table is presented giving the chances of a single specimen being of the specified sex with a given upper canine measurement.

Division of Vertebrate Ecology, Johns Hopkins Univ., Baltimore 5, Maryland. *Received April 2, 1958.*

ADDITIONAL RETURNS FROM FREE-TAILED BATS BANDED IN OKLAHOMA

By Bryan P. Glass

During the past five summers the writer has been banding bats of the species *Tadarida brasiliensis mexicana* taken from brood colonies in northwestern Oklahoma (Fig. 1), hoping that knowledge could be gained concerning their migratory movements. Bands were applied in amounts as follows: 1952, 290; 1953, 23; 1954, 1790; 1955, 4143; 1956, 10,800. The gratifying number of returns received in the latter part of 1956 and in 1957 may be attributed partly to the greater number of bands applied, and partly to the presence in the field of other workers, particularly D. G. Constantine of the U.S. Public Health Service at Carlsbad, New Mexico, and Richard E. Davis of The Johns Hopkins University at Kerrville, Texas, who have recovered and reported many of our bands. A total of 40 band recoveries have been reported since September 1, 1956. Of these, 37 were applied in 1956, and three in 1955. Space will not permit listing by name all of those who have reported bands. Their help, however, is gratefully acknowledged.

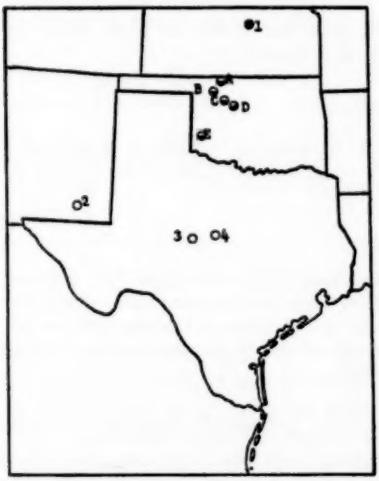

Fig. 1.—Location of five brood colonies in Oklahoma where bats have been banded (half circles). A, Merrihew Cave; B, Selman's Cave; C, Vickery Cave; D, Connor's Cave; E, Reed Cave. Solid circle indicates an August recovery (Emporia, Kansas); open circles indicate September recoveries (2, Carlsbad Cavern, N. Mex.; 3, Ballenger, Tex.; 4, Brownwood, Tex.).

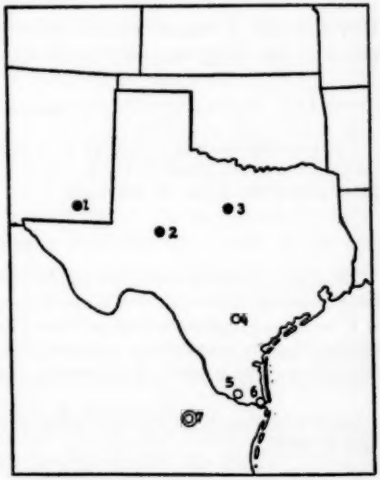

Fig. 2.—Band recoveries for October (solid circles), November (half circle), December (open circle), and January (double circle). Locations are as follows: 1, Carlsbad Cavern, New Mexico; 2, Sweetwater, Texas; 3, Weinert, Texas; 4, Bracken Cave, Texas; 5, McAllen, Texas; 6, Brownsville, Texas; 7, Cueva del Rincon de la Virgen near Monterey, Mexico.

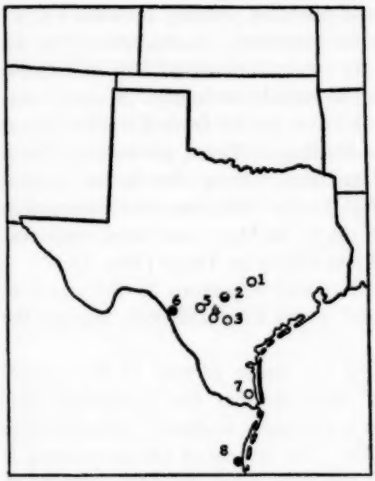

FIG. 3.—Band recoveries for March (solid circle) and April (open circle). The half-circle indicates bands were recovered there in both months. Locations are as follows: 1, Elgin; 2, Ney Cave; 3, Bracken Cave; 4, Frio Cave; 5, Davis Cave; 6, Del Rio; 7, Harlingen, all in Texas; 8, 125 mi. S Brownsville, in Mexico.

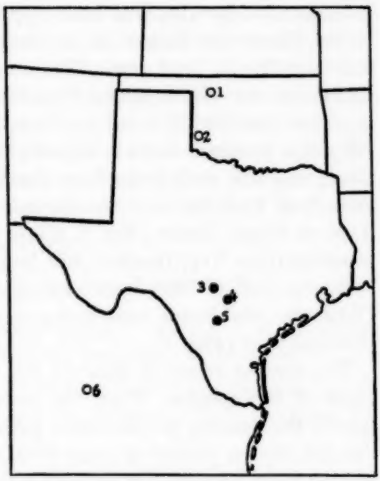

FIG. 4.—Band recoveries for May (solid circle) and June (open circle). Locations are as follows: 1, Selmans Cave, Oklahoma; 2, Reed Cave, Oklahoma; 3, James River Cave, Texas; 4, Ney Cave, Texas; 5, Bracken Cave, Texas; 6, Cueva de Laguna Seca, near Torreon, Mexico.

Two returns have been secured from distant points in Mexico. One, which was banded as a baby on July 10, 1956, was reported from the coast of Mexico 125 miles south of Brownsville (Fig. 3) on March 20, 1957. Another banded on July 14, 1955, was reported from Cueva de Laguna Seca, near Torreon, Coahuila (Fig. 4), on June 1, 1956, the information not reaching Stillwater until October. The first of these fits into a general pattern of fall migration southward and spring migration northward. The second does not fit into any migratory pattern yet indicated by band returns.

Chronologically, the first return recorded was one in late August, from Emporia, Kansas (Fig. 1). The bat was one born in July, and the record is probably only indicative of a general scattering in late summer when numbers were at a maximum. In September, eleven were reported at Carlsbad, New Mexico and one each from Brownwood and Ballenger, Texas (Fig. 1). In October, three were reported from Carlsbad, and one each from Weinert and Sweetwater, Texas (Fig. 2). No returns were received in November of 1956 but a record from the previous year (Glass, 1958) was from Bracken Cave near San Antonio, Texas (Fig. 2). In December, one band was reported from Brownsville and one from McAllen, Texas (Fig. 2). The months of January and February yielded no returns; however, the July 4, 1956, recovery of a band

in Selman's Cave that had been applied the previous January by Villa (1956) in the Cueva del Rincon de la Virgen near Monterey, Tamaulipas (Fig. 2), indicates that at least some Oklahoma bats are in that vicinity in midwinter. In March, one was reported from Mexico, as noted previously. Also one was reported from Del Rio and one from Davis Cave not far from Kerrville, Texas (Fig. 3). In April, one was reported from Harlingen, Texas, seven from Davis Cave, and one each from Ney, Bracken and Frio Caves, also in the general vicinity of Kerrville and San Antonio (Fig. 3). In 1955, one was reported in April at Elgin, Texas (Fig. 3, Glass, *loc. cit.*). In May, one band each was reported from Ney, Bracken and James River Caves in Texas (Fig. 4).

By the end of May bats were again becoming numerous in the caves in Oklahoma, and bands were being recovered where they had been applied the previous year (Fig. 4).

The returns reported here do not reveal the entire picture of the annual cycle of the species. They do, however, indicate that the population that spends the summer in Oklahoma performs a southerly migratory movement in the fall, over a period of some four months. The extent of the movement is not yet fully known, but at least some of the bats reach near the latitude of the tropic of Cancer, while some may go no farther south than the Rio Grande Valley. The reverse happens in the spring with many, but not all, of the animals returning to the same vicinity from which they started out the previous fall.

This behavior fits the generally accepted definition of the term "migratory," and the species may therefore be positively recognized as a migratory species.

All of the bands reported in this account were applied in one or another of the five brood-colonies in Oklahoma. Merrihew, Selman's, Connor's, and Vickery Caves contain what is essentially a single population, as there is evidence of continual population exchange between them. Together these four caves harbor the northernmost brood population of the species in the plains region of the United States. Band returns from this population therefore assume added significance, for the confusing of the indigenous population with transients does not occur as it does in the caves further south, the population being a limital one. The population in Reed Cave cannot be considered limital, as bats banded there have not been found to mix freely with those of the other caves. Bats from the north, however, have frequently been seen in Reed Cave during the fall, when they must be considered to be transients in migration.

The shortest interval of time yet recorded between banding and recapture is 12 days. Four bats banded at Selman's on September 14, 1956, were recovered at Carlsbad on September 26. Another was recovered at Carlsbad 13 days after banding. The airline distance involved is approximately 500 miles. This flight occurred during the fall migration. A less explicable recovery was reported from Randolph Field, Texas, on July 23, 1957, of a female bat found dead which had been banded at Reed Cave on June 28 of the same year. The airline distance in this case exceeds 400 miles, and the time of year coincides with

the peak of reproductive and nursing activity, when females might be expected to be most sedentary. Unfortunately there is no information as to whether or not the bat had lactated.

Among the numerous banded bats recovered in June, 1957, from the caves in northern Oklahoma were a number of known age, the bands having been applied when the bats were still too young to fly. Females known to be less than 12 months of age were uniformly found to be pregnant. In bats of this species, therefore, females attain full sexual maturity during their first year.

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Dept. of Zoology, Oklahoma State Univ., Stillwater. Received May 5, 1958.

FOODS OF THE INDIAN FALSE VAMPIRE

BY ISHWAR PRAKASH

Many interesting observations on the food of the Indian false vampire bat, *Megaderma lyra lyra*, have been recorded in the past. Aitken (1907) observed the bat eating a sparrow. Gleadow (1907) wrote that the vampires live on birds and mice. Green (1907) found remains of small birds (*Osterops, Cinnyris*) in his veranda and attributed their consumption to vampire bats. Primrose (1907) added the Indian bush-chat, *Pranticola maura*, to the menu of *Megaderma lyra lyra*. Mosse (1931) witnessed a fair-sized lizard being eaten by the bat. McCann (1934) found a vampire eating a pipistrel. Phillips (1922) observed that two male vampires, in a large case, devoured a dwarf pipistrel, *Pipistrellus mimus*, which was put in with them, consuming everything except the wing membrane. They also consumed a dead mouse and part of a young gerbil. Blanford (1888–91) wrote that false vampires feed on smaller bats, grasshoppers and crickets, but that frogs appear to constitute their chief diet. Prater (1948) observed that they prey on small animals—smaller bats, for example—on birds, frogs and even fish. Grasshoppers and crickets are also eaten.

During the last few years some observations were made on the habits of this bat. In a colony at Jodhpur, the vampires have many times been observed

scrunching other bats, *Rhinopoma kinneari, Rhinopoma hardwickei* and *Taphozous perforatus*. The victims were always held by their heads and only their heads were eaten, as we collected many headless bats from the colony. On other occasions vampires were observed carrying off a wall lizard, *Hemidactylus flaviviridis*, from the shade of a lighted electric bulb in the veranda. Once a false vampire was observed hanging in our veranda (at Jodhpur) at 10 PM. It had a full-grown sparrow in its mouth. The bird was held by the head. The process of feeding was observed till 11 PM, when I slept. The progress of eating was slow but very steady. Next morning the wings of the bird were found in the veranda. After two nights a bat was again seen at the same place with an insect, *Schizodactylus monstrosus*. The insect was identified by its dropped parts next morning. On another night a false vampire was again hanging at the same place with a *Taphozous perforatus* in its mouth. Only the head was eaten and the remaining body was removed from the veranda next morning.

During the course of studies on the mammals of the desert of Rajasthan, India, captive vampires were fed on birds, gerbils, mice, rats and other bats. They were kept in large cages (90 × 30 × 30 in.) and the food was given to them after dusk. They were observed until 10 PM and the results were noted next morning. The experiments were carried out with several batches of bats. No interest was taken in items that were dead (sparrow, bush-chat and house mouse, recently chloroformed), although Phillips (1922) observed vampires feeding on a dead mouse. Reactions to living foods offered are listed below.

House sparrow, *Passer domesticus*.—The bird, on the floor of the cage, was attacked by one of the largest bats with the wing membranes widespread. The bat caught the head of the bird in its jaws and, clinging to the mesh of the cage, began its dinner. Other bats tried to share the kill but were not allowed to do so.

Bush-chat, *Saxicola caprata*.—This bird was killed like the sparrow and was consumed by one bat only. Wings and claws were left.

Indian desert gerbil, *Meriones hurrianae*.—The 70-mm. gerbil was furiously attacked when introduced into the cage. As it moved, it was attacked by half a dozen vampires, but the swiftest bat picked it up and clung to the mesh of the cage with it. Other bats attacked, and the gerbil was dropped and seized by another bat. The quarrel continued for half an hour after which the bats subsided and one of them ate the gerbil. The next morning the gerbil's body was consumed up to the front legs. It remained in the cage all day, but was not eaten further.

House mouse, *Mus musculus*.—A mouse was attacked, killed and eaten up to the hind limbs.

House rat, *Rattus rattus*.—A rat was attacked on the head when introduced into the cage; after fighting for 3 minutes with one bat it escaped and climbed up the mesh of the cage, thus disturbing all the bats. The next morning the

rat and one vampire were dead, the rat with a badly injured head and the bat with a deep wound in the breast.

Bats, *Rhinopoma kinneari, R. hardwickei* and *Taphozous perforatus.*—Only the heads of these bats were eaten; *Taphozous* was preferred. Phillips (1922) observed that only the wing membrane of a pipistrel was unconsumed.

Stomach contents.—The stomach contents of 20 bats were examined. Care was taken to collect these bats just after their feeding time. The contents included remains of insects, bony pieces of amphibians, bones of fishes and bats, scales (1.5 mm.) of fishes, and the entire alimentary canal of a fish (?).

These observations were made in connection with a project, "Study of the Vertebrates of the Desert of Rajasthan, India," sponsored by UNESCO. The author is indebted to UNESCO for a liberal financial grant and to Dr. Daya Krishna for guidance.

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HEMATOLOGICAL CHANGES WITH TORPOR IN THE BAT

By PHILIP H. KRUTZSCH AND A. H. HUGHES

The fact that many physiological conditions are accompanied by a variation in the blood composition has led investigators to study the effect of hibernation on the composition of the blood. Lidicker and Davis (1955) suggest that the ability of the poikilothermic bat to enter and leave the torpid state rapidly and seemingly at will may be a function associated with the storage of erythrocytes in the spleen. They suggest that the mass release of such stored cells may influence the oxygen supply to the tissues which in turn may be one of the factors stimulating the heart to greater activity, thus assisting in the arousal of the bat from the torpid state. There is a remarkable reduction in the

peripheral red cell population in the blood of hibernating bats; however, the erythrocytes are returned to the peripheral circulation (from storage?) in a matter of minutes. Thus, the wide discrepancy between blood counts in the active and torpid bat must be entirely a matter of distribution rather than an actual shift in the number of blood cells in response to temperature. Other students of bat hibernation, Worth (1932) and Evans (1938), have noted that the spleen is larger in winter than in summer and suggest that this enlargement is the result of engorgement of the spleen by red blood corpuscles.

Rasmussen (1916) and Mann and Drips (1917) report similar splenic enlargement during hibernation in the woodchuck and ground squirrel. They feel that the splenic enlargement is the result of engorgement of the spleen by erythocytes. Rasmussen notes that the number of leucocytes increased greatly in woodchucks aroused to semidormancy during hibernation and that the red cells exceeded the counts for active animals. He suggests that such variations in the number of red cells are dependent, to a large extent, upon the concentration of the blood (water volume) and the redistribution of the corpuscles (from the spleen or other members of the reticulo-endothelial system to the peripheral blood?).

Suomalainen and Granstrom (1955) studied hematological changes in hibernating hamsters. They found a slight increase in the red cell count and a marked decrease in the white cell count in hibernating animals. They speculated that, since cold and starvation are essentially associated elements in hibernation, and because these elements elicit a strong general adaptation syndrome (Selye, 1950), perhaps changes occurring in the ratios of different blood cells can be taken as indicators of the general adaptation syndrome caused by the cold. According to Selye, the counter-shock phase of the alarm reaction is characterized by neutrophil leukocytosis, eosinopenia and lymphopenia. The values obtained for the golden hamster are typical of stress, i.e., leuko-, eosino- and lymphopenia and neutrocytosis. These values were obtained in spite of the short (3 day) hibernating cycle and lightness of torpor. The lower the body temperature of the hamster, the more marked are the lymphopenia and

TABLE 1.—*Spleen dimensions*

	Tadarida b. mexicana		*Myotis velifer*	
	Active	Torpid	Active	Torpid
	12.0	19.0	13.5	17.0
	14.0	16.0	12.5	19.5
	14.0	16.0	12.0	18.0
	11.8	18.5	14.0	20.5
	11.0	18.5	12.0	20.0
	11.0	17.0	15.0	20.5
	12.0		13.0	
			14.0	
Avg.	12.0	17.3	13.2	19.1

TABLE 2.—*Erythrocyte counts* ($\times 10^{-3}$)

BAT IN ACTIVE STATE (cells per mm³)		BAT IN HIBERNATING STATE (cells per mm³)	
Tadarida b. mexicana:		*Tadarida b. mexicana:*	
	9,700		3,300
	12,360		2,670
	14,560		9,260
	10,020		4,240
	9,300		7,500
	8,120		2,240
	10,500		10,030
Avg.	10,651	Avg.	5,591
Myotis velifer:		*Myotis velifer:*	
	8,400		5,450
	11,380		6,380
	11,880		5,500
	13,920		6,200
	9,980		7,940
	11,800		10,170
	10,800		
Avg.	11,151	Avg.	6,926

neutrocytosis. The elevated red cell counts during hibernation were suggested as due to reduced water content of the blood.

Our preliminary studies on the population of the various formed elements in the peripheral blood of torpid and active bats suggest that observed changes in these populations are the result of temporary systemic storage rather than hypo- or hyper- hemopoietic activity in response to stress.

Materials and methods.—Blood counts and spleen examinations were performed on both active and hibernating bats. The bats (*Tadarida braziliensis mexicana* and *Myotis velifer incautis*) used in these studies are closely related to the species reported upon by Lidicker and Davis (1955) and Worth (1932).

The animals were obtained on August 7, 1957, from the Davis Blow-out Cave, near Fredericksberg, Blanco County, Texas. The bats were kept in cages and readily accepted food and water when active; no change in body weight was noted. Individuals were harvested daily, and all were killed by the ninth day after their capture. Some animals were maintained at temperatures of 80–85°F. and remained fully active; others were kept at temperatures of 40–45°F. and were rendered torpid. Blood samples were taken directly from the heart with a heparinized syringe. Active bats were lightly anesthetized with ether, and the heart was exposed for bleeding by excision of the sternum. Hibernating (torpid) bats were bled in a similar fashion but without benefit of anesthesia. Prior to bleeding, the spleen of each individual was measured. The following hematological procedures were done on each blood sample: A red cell count (blood diluted 1:200 with Hayems solution and counted in the Neubauer counting chamber); a white cell count (blood diluted 1:20 with a 1.0 per cent solution

of glacial acetic acid and counted in the Neubauer counting chamber); a differential white cell count (determined from thin smears made on slides and stained in the usual fashion with Wright's stain); and platelet (indirect) and reticulocyte counts (obtained by the Dameshek method; cf. Wintrobe, 1956). Several counts were made on each individual.

Results.—Our data (Table 1) indicate that the spleens of active bats are approximately 25 per cent smaller than those of hibernating bats. We found that the spleen returns to its normal, active dimensions rapidly when the bats are transferred from the cold to the warm environment. Changes in spleen dimensions are less rapid in *Tadarida b. mexicana* than in *Myotis velifer*. There is considerable individual variation in the time required to pass from the engorged state of the spleen, as seen during torpor, to the unengorged condition of the active spleen. A similar temporal variation exists where the spleen passes from the unengorged to the engorged state.

Seven active *Tadarida* were placed in a refrigerator at 40°F.; individuals from the group were killed at intervals to determine the approximate time required by the spleen to reach engorgement. Two bats were killed after 1 hour and 30 minutes; the spleen of one was typical for the active state, pale-red and 11.0 mm. long. The spleen of the other was rounded, dark-red and 16.0 mm. long, approaching the condition of the spleen in torpid bats. Two other bats were harvested after 2 hours. The spleen of one was slightly rounded and 12.0 mm. long; that of the other was engorged and 16.0 mm. long; both were dark-red. The remaining three bats were killed and autopsied after 3 hours at 40°F. The spleens of these individuals were 17.0 mm., 18.5 mm. and 19.0 mm. in length; they were engorged and dark-red (typical of the torpid condition). The spleen in *Tadarida b. mexicana* responds less rapidly to changes in temperature than does that of *Myotis velifer*. Lidicker and Davis also found considerable individual variation in the splenic dimension in torpor of the closely related *Tadarida braziliensis cynocephala*.

Five active *Myotis velifer* were placed under similar conditions. Two bats were killed after 1 hour and 30 minutes; their spleens were partly engorged, dark-red and measured 15.0 mm. and 17.0 mm. in length (approaching the torpid condition). The remaining three bats were killed and autopsied after 2 hours and 40 minutes; their spleens were all dark-red, engorged and 18.0, 19.5 and 20.5 mm. in length (typical of the hibernating condition).

The spleens in both species respond to lowered temperatures by becoming engorged with blood. Spleen weights were not taken; however, the increased size during torpor suggests an increase in the weight of the organ. Weight increases up to 500 per cent have been pointed out by Lidicker and Davis for *Myotis sodalis*.

Erythrocyte Counts.—There is a marked reduction in the red cell population of the circulating blood in the torpid bats that were studied. Counts (Table 2) of erythrocytes in the peripheral blood of torpid animals indicate that there is a decrease in the red cells of approximately 45–50 per cent for *Tadarida b.*

mexicana and 30–35 per cent for *Myotis velifer*. These findings agree with those of Lidicker and Davis (1955), who have demonstrated a 41 per cent decrease in the number of red cells in the blood of torpid *Myotis sodalis*. Worth (1932) found red cells more numerous in the blood of bats (*Myotis lucifugus*) collected in December than in those collected in July. These "winter bats" from which Worth obtained blood were not torpid. If we keep in mind the very rapid return of the erythrocytes to the peripheral circulation following arousal from torpor, it is apparent that the blood from these "winter bats" is not comparable to that of the hibernating state. Perhaps the discrepancies between Worth's winter and summer erythrocyte counts may indicate individual variation rather than a variation in response to temperature changes.

The erythrocyte counts presented by Martinez (1939) for *Tadarida brasiliensis* taken in November in the State of Guerrero, Mexico, are somewhat higher (13–15 million per mm.^{3}) than are ours for *Tadarida b. mexicana* (8–14.5 million per mm.^{3}). Since Martinez does not state the metabolic condition of his bats, we cannot compare our data with his. Perhaps the differences related to species, since variation due to season should be slight (the November climate in Guerrero—average mean temperature, 73°F.—is almost comparable to the August climate of south-central Texas—average mean temperature, 78°F.).

Platelet counts.—Rasmussen (1916), in his studies of blood in the woodchuck during hibernation, found that platelets were equally abundant at all seasons. We find that there is a decided decrease in the number of platelets in the peripheral blood of bats during the torpid state (Table 3). This decrease

TABLE 3.—*Indirect platelet counts*

BAT IN ACTIVE STATE (cells per mm^3)		BAT IN HIBERNATING STATE (cells per mm^3)	
Tadarida b. mexicana:		*Tadarida b. mexicana:*	
	70,320		74,080
	116,400		72,080
	185,400		250,000
	611,520		44,000
	100,200		
	81,200		
	87,500		
Avg.	178,934	Avg.	110,240
Myotis velifer:		*Myotis velifer:*	
	150,000		87,340
	204,800		223,740
	141,600		93,860
	226,640		73,400
	139,720		60,000
	435,400		
	361,080		
Avg.	224,055	Avg.	107,668

(52 per cent for *Myotis velifer* and 39 per cent for *Tadarida b. mexicana*) is in keeping with the general reduction of all formed elements in the peripheral blood during torpor. Presumably the platelets are retained in the spleen along with the red cells. The number of platelets in the peripheral blood increases rapidly when the bat is aroused from torpor.

Our evidence conflicts with that of Worth (1932), who was impressed by the fact that platelets, although not counted, appeared on the blood smears in about the same numbers as in normal human blood. Not only did we find fewer platelets in torpid bats, but the highest count obtained by us (224,055 from an active *Myotis velifer*) is considerably below the normal human values (500,000–900,000).

Although clotting experiments were not carried out on the blood of these bats, it seems likely that clotting time would be increased in torpid animals since platelet counts are significantly lower during torpor. This relationship is in keeping with the general lowering of metabolic activity in torpid animals.

Leucocyte counts.—The number of circulating white corpuscles in the torpid animals decreased to approximately 62 per cent of the active count in *Tadarida b. mexicana* and to approximately 32 per cent of the active count in *Myotis velifer*. These figures are in keeping with the lowered counts of all formed elements in the torpid animals. The total white cell population varies between the two species (Table 4). In both torpid and active metabolic states, white cells are more numerous in *Myotis velifer*. Our average white cell counts are

TABLE 4.—*Leucocyte counts*

BAT IN ACTIVE STATE (cells per mm³)		BAT IN HIBERNATING STATE (cells per mm³)	
Tadarida b. mexicana:		*Tadarida b. mexicana:*	
	1,850		500
	800		700
	300		450
	500		350
	900		700
	700		150
	500		
	500		
Avg.	762	Avg.	475
Myotis velifer:		*Myotis velifer:*	
	1,750		500
	1,100		1,550
	3,800		400
	800		800
	1,450		650
	1,050		1,000
	4,500		
	2,750		
Avg.	2,500	Avg.	817

TABLE 5.—*Differential leucocyte counts for four active Myotis velifer*

LEUCOCYTES	BAT A	BAT B	BAT C	BAT D
Lymphocytes	30%	34%	54%	64%
Monocytes	2%	2%	1%	0%
Myelocytes	7%	6%	7%	12%
Neutrophils	59%	58%	36%	22%
Eosinophils	2%	0%	0%	0%
Basophils	0%	0%	2%	2%
Total leucocytes	4,500/mm³	2,750/mm³	1,450/mm³	3,800/mm³

considerably lower than those of *Myotis lucifugus* (Worth, 1932) and of *Tadarida braziliensis* (Martinez, 1939). In spite of the possibility of physiological aberration, the striking reduction in the number of white corpuscles in torpor is a constant phenomenon.

Because of the extremely low white cell population in the hibernating animals of both species, differential counts were not possible. Differential counts were obtained for active *Myotis velifer*, but not for *Tadarida*. In spite of the fact that the *Myotis* sample is too small (4 counts) to be significant, there is uniformly an elevation of the granulocytic series. Many very large macropolycytes of the type typical in pernicious anemia in man were seen in each sample. The significance of the macropolycytes is not undertood, but such cells are rarely seen in health. Table 5 gives the types of cells and the percentage of each in the four counts.

Reticulocyte counts.—The reticulocyte counts of both species of bats show a very slight increase in the active over that in the hibernating state. The average count of .27 per cent for torpid *Tadarida* increased to an average of .33 per cent following arousal. In *Myotis*, the number of reticulocytes increased from .10 in torpor to .18 per cent in the active state. The slightly higher reticulocyte population following arousal suggests a similar increase in erythrocyte production. These slight changes in reticulocytes support the view that the tremendous increase in red cells following arousal from the torpid state is due to a release of erythrocytes trapped in the spleen (and possibly other organs of the reticulo-endothelial system) rather than from a tremendous post-hibernatory hemopoietic effort.

SUMMARY

A general decrease in the circulating population of all formed elements of the blood characterizes hibernating bats. This reduction accompanies the generally decreased metabolism of these animals and the correspondingly reduced requirements for anti-inflammatory, clotting and oxygen-transport mechanisms. The actual physiological factors involved in these reductions are unknown. It may be postulated that at least the erythrocytes and platelets are trapped in the spleen (and possibly other organs of the reticulo-endothelial system) during periods of torpor. These constituents are again released to the peripheral circulation when the animal becomes active.

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WEIGHT PATTERNS AND HIBERNATION IN *TAMIAS STRIATUS*

BY JOSEPH ALLAN PANUSKA

Although the eastern chipmunk, *Tamias striatus*, is a familiar occupant of the forests and fields of eastern North America, there have been no extensive studies of its hibernation. In numerous brief literature citations, expressions such as hibernator, light or deep hibernator, torpid, semitorpid, and similar terms may be found, but clear distinctions between these degrees of reduced physiological activity have not been drawn. As a result, our knowledge of the hibernation of *T. striatus* is confused. Perhaps because of this confusion, major reviews of hibernation such as those of Johnson (1931), Kayser (1950), and Lyman and Chatfield (1955) fail to mention the chipmunk.

The present experimental study, following two years of preliminary work and complemented by related ecological investigations (Panuska and Wade, 1956, 1957), was conducted from 1954 until 1956 at St. Louis University. Its objective was to determine whether this species has an annual weight cycle resembling that of most hibernators, and whether its hibernating habits are as irregular as scattered reports of the literature indicate.

Inasmuch as previous accounts represent observations on relatively small groups of animals from all parts of the eastern United States, I determined to study large numbers from one region. Waupaca, Wisconsin, where the chipmunk is abundant, was selected as the site. Most of the chipmunks collected there appeared closely related to *T. s. griseus,* but some resembled *T. s. lysteri* and still others seemed to be intermediates. The ranges of these two subspecies have long been known to overlap in this central Wisconsin region (Howell, 1929); hence it appears unnecessary to attempt subspecific designation.

I am much indebted to Nelson J. Wade of the Biology Department of St. Louis University, whose interest and guidance made the completion of this project possible.

REVIEW OF LITERATURE

Knowledge of the hibernation of an animal comes from several sources: weight patterns suggesting a relationship to known hibernating species, food-storing habits, dates of winter disappearance, and physiological data which reflect temperature-control mechanisms. More directly, hibernation may be observed in nature or in the laboratory.

Weight cycle.—It is generally believed that *T. striatus* lacks a prominent annual weight cycle, that is, a cycle of gaining weight in the autumn and of losing it during the late winter as has been frequently reported for *Citellus tridecemlineatus.* Rhoads (1903), Stone and Cram (1905), Howell (1929), and Seton (1929) reported that the animal does not become obese before retiring to its burrow in the autumn. Although isolated weights of a few animals have been given by Schoonmaker (1928), Bailey (1929), Howell (1929), Odum (1949), and Engels (1951), apparently no studies include a series of consecutive weights sufficient to suggest a cycle. Woodward and Condrin (1945) found seasonal variations in blood-sugar concentrations and in the weight of adrenals, but did not mention body weights.

Food-storing habits.—Extensive burrow systems of the chipmunk have adequate space for food storage, and *de facto* much food is stored in the fall. The name *Tamias,* Greek for "housekeeper," indicates this propensity. Stone and Cram (1905) and Howell (1929) interpreted this food-storing habit as an indication that the animal is not a true hibernator.

Winter disappearance.—During the winter months, there is a general disappearance of *T. striatus* from above ground, yet the occasional winter appearance of individuals has been noted in all parts of its range. Dates of disappearance and emergence vary considerably, and the relation of these dates to temperature is disputed. Cory (1912), Goodwin (1935), and Preble (1936) related the disappearance to the severity of the winter, while Smith (1931) and Williams (1936) presented evidence which indicated independence of temperature.

Schooley (1934), Hamilton (1943), Cahalane (1947), and Manville (1949) report that males emerge earlier than females. No citations indicating an earlier female emergence were found.

Observations in nature.—These are quite rare and are usually unsatisfactory because of incomplete descriptions. Generalizations have been made which indicate almost all types of hibernating activity.

Observations under controlled conditions.—Allen (1938) maintained several dozen animals under various conditions and observed "every gradation between fully active chipmunks and wholly torpid ones . . . during the winter season." She also noted frequent awakenings, even during periods of hibernation. Condrin (1936) made similar comments and added that, while generally the eastern chipmunk is not a "deep hibernator," it must "very definitely be classified as a hibernating form." Later, Woodward and Condrin (1945) described the responses of chipmunks that they considered to be torpid. Temperatures below 16°C. occurred only in those animals that did not survive. Their "torpid" animals had rectal temperatures of 16.8° to 29.0°C. and depressed respiratory rates of 23 to 60 per minute. The conditions they described correspond only to semitorpidity as defined in this study.

Two recent workers suggested a high winter mortality. Linduska (1950) reported that only 10 per cent of the animals marked in any given year were captured the following year, and Yerger (1955) estimated an over-all average annual survival of 45 per cent.

When Engels (1951) observed that some individuals remained below ground for as long as 25 weeks at a time, he concluded that they hibernated extensively. He proposed that there might be "an inherent annual cycle, more or less independent of the environment." Engels was speculating on his own somewhat limited observations and on the previously mentioned seasonal variations that were listed by Woodward and Condrin.

MATERIALS AND METHODS

During the four years of experimentation, 229 *T. striatus* were used. The conditions of the two major series of experiments, referred to as Series I and Series II, are given in Table 1. The preliminary efforts, although helpful in developing method, are not included.

Animals were maintained in rooms which were warm, unheated, or cold. The warm room, kept at 20°C., was lighted mainly artificially for about 10 hours a day. The unheated room, with its temperature varying as shown in Fig. 1, admitted some natural light, but irregular artificial lighting was also used. The cold room, a 6-foot cube, was kept dark except during brief periods of inspection. Routine checks were made with a flashlight in order to minimize disturbance. The temperature, shown in Fig. 1, was maintained within 0.5°C.

Animals were kept separately in burrow-boxes or wire-mesh cages provided with small nesting boxes. Purina laboratory chow and water were plentifully available except during certain special experiments. Body temperatures were taken rectally by thermocouple. The chipmunks were weighed every week, but they were observed visually every one or two days, usually daily. Their condition was recorded as follows: (1) *active:* awake or in normal sleep, respiration over 60 per minute; (2) *semitorpid:* respiration between 20 and 60,

TABLE 1.—*Hibernation experiments*

	NUMBER OF ANIMALS	DATES OF EXPOSURE TO COLD
SERIES I:		
Sept. 1954 to June 1955	5	Warm room, entire time.
	25	Cold room, Sept. 17 to Oct. 15; unheated room thereafter.
	88	Cold room, Sept. 17 to June 14, except for interruption from Oct. 15 to Nov. 5.
	15	Cold room, Sept. 17 to Oct. 15; unheated room, Oct. 16 to Dec. 1; cold room, Dec. 2 to June 14.
SERIES II:		
Sept. 1955 to June 1956	8	Warm room, entire time.
	51	Cold room, Sept. 13 to June 21.

not readily disturbed by a gentle movement of the cage or by dropping sawdust on back; (3) *torpid:* respiration below 20.

A little sawdust was placed on the backs of torpid and semitorpid animals.

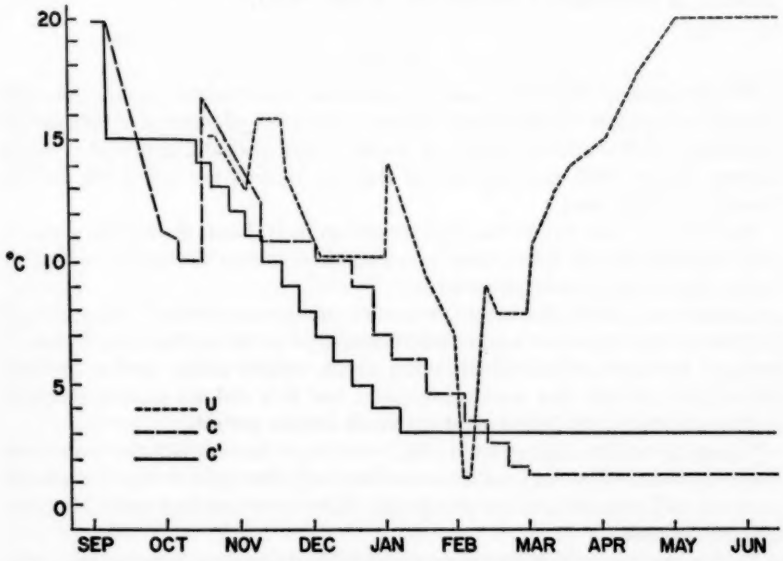

FIG. 1.—Air temperature variations in the unheated and cold rooms. Curve *U*—1954–55 unheated room temperatures; this is based on daytime readings and does not show daily variations. Curve *C*—1954–55 cold room temperatures. Curve *C'*—1955–56 cold room temperatures.

If this was disturbed at the time of the next observation, it was assumed that the animal had moved from its sleeping position. Judgments concerning activity were often related to water and food consumption and to the presence of feces in trays placed beneath cages for sanitary purposes.

It is probable that some of the judgments concerning semitorpidity are faulty; any closer check, however, such as made by more violent movements or by the taking of body temperatures, would have caused additional disturbance and did not seem desirable. Ordinary laboratory conditions are sufficiently disturbing to the chipmunk, and in order to obtain an accurate behavioral picture, handling must be minimized.

In order to determine how much the required handling of refrigerated animals affected their hibernating behavior, several were kept in burrow-boxes with an opportunity to live in a manner more closely resembling their natural habitat. These animals were neither weighed regularly nor were their temperatures taken. Their behavior did not prove exceptional.

As indicators of the constancy of our laboratory conditions, one *Citellus tridecemlineatus* and 14 *Mesocricetus auratus* were refrigerated under the same conditions. Since a considerable amount of research has already been done on these two species, it was hoped that "normal" behavior on their part would indicate an absence of any strongly disturbing elements in the conditions. Both behaved as anticipated (Panuska and Wade, 1958).

RESULTS

Weight cycles.—Figures 2 and 3 summarize the weight cycles. All cold-exposed groups lost weight initially during a period of adjustment to refrigerator conditions. Cold-exposed groups in Series I were partially deprived of water during March, 1955, and because of this the records are not given beyond March 4 in that year.

We were not able to continue the weighings in St. Louis during the summer, and therefore do not know from our own observations if there is a summer cycle; this would appear doubtful.

It should be noted that even the warm-room groups showed cycles, though these were of a depressed nature when compared to the cycles of cold-exposed groups. Warm-room individuals often attain weight *peaks* similar to those attained by animals that were refrigerated, but they did not gain as promptly and maintained their high weight for much briefer periods.

Comparative data for animals that were kept in captivity for two years under similar or different conditions tend to verify the opinion that the average gains of cold-exposed animals are greater than corresponding gains of warm-exposed animals.

During any one year, there were considerable differences between the cycles of individual animals, some showing gains in the order of 35 per cent over an early September weight, others showing no pattern of increase at all.

The presence of a weight cycle appears to be related to hibernation. During

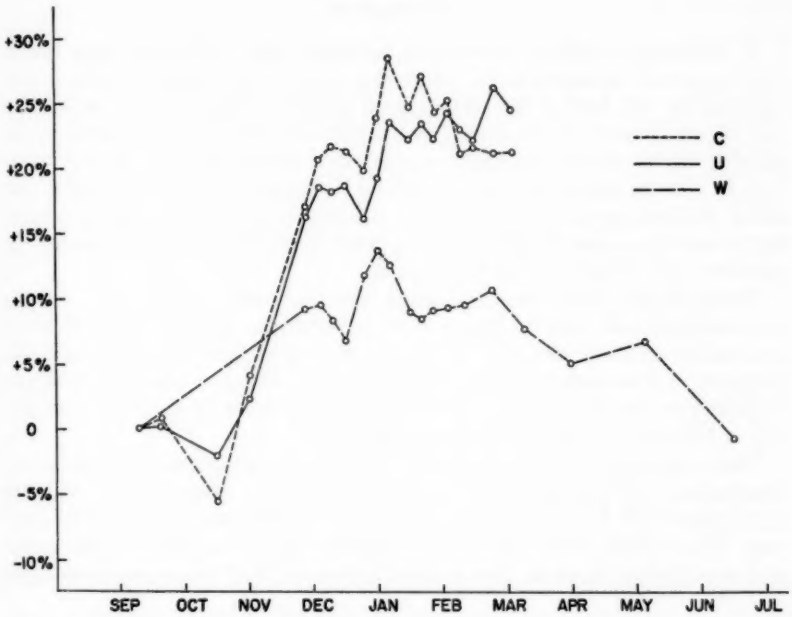

FIG. 2.—1954–55 weight cycles plotted according to percentage gained or lost over the first recorded September weight. Based on averages. Curve *C*—44 refrigerated animals (avg. wt. on Sept. 8: 117.3 gm.). Curve *U*—14 animals in unheated room (avg. wt. on Sept. 8: 113.6 gm.). Curve *W*—5 warm room animals (avg. wt. on Sept. 8: 115.2 gm.). All of the listed animals survived the plotted period.

Series II, for example, no animal lacking a weight cycle hibernated for a prolonged period, although one achieved torpor briefly. Of four animals that had slight cycles, three did not achieve torpor. Among those having prominent cycles, 85 per cent became torpid, most of these for extended periods. Ninety per cent of all cold-exposed groups, whether they hibernated or not, had weight cycles.

A consideration of dates when the weights of individual animals began to decline showed that several weeks of declining weight ordinarily preceded the first observed hibernation (usually semitorpor). This indicates a physiological change, perhaps immediately preparatory to hibernation, although there were no other signs of the impending lethargy. In no case did any degree of hibernation precede the weight decline. Hibernation did not end when an individual's low weight was ultimately reached, but usually continued into what might be described as a "plateau" period. These plateaus do not appear on curves which are based on averages of many animals.

Hibernation

1. *Incidence.*—Table 2 summarizes pertinent data. Although deep torpor was frequently encountered in chipmunks, even for prolonged periods, it was attained by only half of the cold-exposed animals. Many degrees of activity and inactivity were noted during the hibernating season. Some animals, remaining active during the entire experimental period, showed no degree of torpor. Certain individuals occasionally or frequently became semitorpid, but never attained torpor. Many were often semitorpid and occasionally torpid. Some were frequently torpid, either for brief scattered intervals or, except for periodic awakenings, for several months.

During Series I, from January through May there were usually three animals in semitorpor and three in torpor at each visitation. During Series II there was greater monthly variation. Until early February there were only scattered instances of hibernation; March had the highest incidence with usually three in semitorpor and 12 in torpor. There was a slight decline in April and a greater one in May; all but two were active after June 9.

There appeared to be no correlation between the age of mature animals and hibernation, both young and old responding in similar irregular patterns. The only animal that was refrigerated for three years hibernated extensively each year. Five animals were kept in the unheated room during Series I and in the cold room during Series II. One of these hibernated both years; two hibernated

TABLE 2.—*Summary of behavior of cold-exposed chipmunks*

	SERIES I, 1954–55				SERIES II, 1955–56	
	No. C*	% C	No. U†	% U	No.	%
No. of animals cold-exposed during hibernating season‡	45		26		40	
No. active throughout entire experiment	15	33	10	39	7	18
No. which achieved only semitorpor	14	31	4	15	7	18
No. which achieved torpor at least briefly	16	36	12	46	26	65
No. torpid for extended periods§	8	18	7	27	23	58
Date of earliest torpor	Jan. 24		Dec. 19		Dec. 29	
Date of latest torpor	May 30		May 20		June 15 (interrupted)	
Period of greatest incidence of torpor	Feb. through May were similar, usually 6 animals in semitorpor or torpor				March and April, usually 13 to 15 animals in semitorpor or torpor	

* C = maintained in cold room.
† U = maintained in unheated room.
‡ Considered as beginning Dec. 1; note, however, that all of these animals were cold-exposed from Sept. on.
§ Torpid for at least a 2-week period, except for periodic awakenings; these animals are also included under "No. which achieved torpor at least briefly."

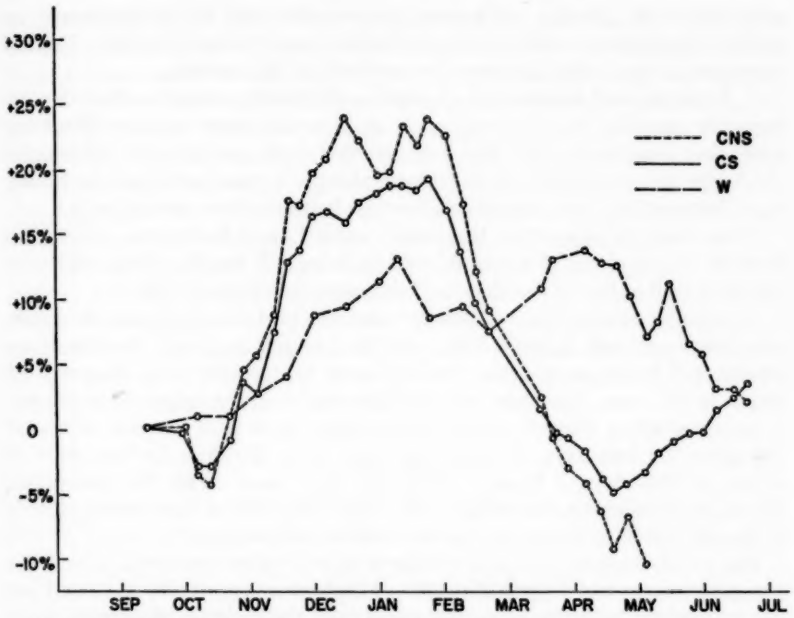

FIG. 3.—1955–56 weight cycles plotted according to percentage gained or lost over the first recorded September weight. Based on averages. Curve *CNS*—20 to 4 refrigerated animals which did not survive the entire experimental period (avg. wt. on Sept. 13: 119.0 gm.). Curve *CS*—21 refrigerated animals which survived the plotted time (avg. wt. on Sept. 13: 121.1 gm.). Curve *W*—8 warm room animals which survived the plotted time (avg. wt. on Sept. 13: 124.3 gm.).

the first year but not the second; two hibernated the second year but not the first. Engels had also noted this latter type of variation.

In no case did starvation or dehydration induce hibernation. Their effects were, rather, a great weight loss, unrest of animals, and (if prolonged beyond a few days) death.

During the spring, several animals in the warm room were found in what appeared to be a semitorpid state. One such animal in particular frequently showed signs of deep semitorpidity inasmuch as it was very sluggish in responding to tactile stimuli and often had a respiratory count of 20–30 per minute. Such behavior is not uncommon in other hibernating species during the dormant period. This individual had hibernated during its previous year of captivity when it was refrigerated.

Mortality during the experiments was high, especially at the beginning of exposure. During Series I, 37 per cent died before October 15, 22 per cent after that date. The early deaths, however, were increased by an unidentified infection. During Series II, 22 per cent died before December 1 and 18 per cent

after that date. During preliminary experiments early deaths frequently resulted if animals were suddenly exposed to low temperatures (0–4°C.). Gradual exposure is apparently necessary for survival in this species.

2. *Inception and termination of torpor.*—Ordinarily a week or two of semitorpidity preceded the first torpor. In no case did torpor occur without any preceding semitorpor. This fact indicates that most animals enter hibernation gradually, but arousal is likely to be more abrupt. Lyman and Chatfield (1955) have discussed the physiological differences between these two processes.

There was no suggestion that males arise from hibernation earlier than females. Eight of the 12 chipmunks which were still torpid in May 1955 were males, as well as five of the nine that hibernated into June of 1956.

3. *Periodic awakenings.—T. striatus* awakens periodically during its torpor, sometimes eats and drinks a little, and then returns to sleep. Periods of uninterrupted torpor were brief. During Series II, torpidity was observed 472 times; in 236 cases, there had been an interruption in the torpor since the previous observation. Torpor without interruption for at least one day was noted 110 times; for two days, 69 times; for three days, 42 times; for four days, 11 times; for five days, 3 times; and for six days, once. With few exceptions, semitorpid animals awoke at least once every day; that is, they were regularly awake at least once during the period between observations.

The visible arousal process is similar to that of other terrestrial hibernators noted by Lyman and Chatfield (1955). Respiration is gradually increased and the first efforts at bodily movement come from the forelegs; shivering accompanies these efforts. The duration of the process apparently depends on the initial depth of torpor and the specific means of arousal. A thorough study of the details of arousal was not made.

4. *Body temperature.*—A summary of temperatures is given in Table 3. The majority of these were taken in late April. Semitorpid animals had temperatures consonant with their degree of lethargy. No consistent sexual differences were noted.

5. *Respiration.*—Respiratory rates varied between the extremes of the hibernating state and rates too rapid for visual counting. Torpid animals displayed

TABLE 3.—*Rectal temperatures*

	NUMBER OF ANIMALS	TOTAL NUMBER OF READINGS	AVG., °C.	RANGE, °C.	STANDARD DEVIATION
Active animals in warm room, 20°C.	13	52	38.5	35.0–41.1	±1.17°
Active animals in cold room, 3°C.	24	75	37.6	32.2–40.0	±1.53°
Semitorpid animals in cold room, 3°C.	6	6	13.2	7.8–20.6	———
Torpid animals in cold room, 3°C.	13	41	6.0	5.0– 7.2	±0.77°

an interesting periodicity in their respiratory movements similar to Cheyne-Stokes respiration found in some other mammals. A study of kymograph tracings of these movements showed that one or two minutes of apnea regularly recurred following periods of relatively frequent respiratory movements, usually 10–20 per minute. During the period of respiration the successive intervals were short at the beginning and gradually increased until apnea set in. This periodicity was observed in eight torpid chipmunks. Hints of periodicity were also given by some semitorpid animals, but since the semitorpid are so easily disturbed, we do not believe the records worthy of inclusion here.

Sometimes apparently normal sleep occurred with movements below 60 per minute. For this reason, as suggested earlier, the data concerning semitorpidity must not be interpreted absolutely except in cases where body temperature or reaction to stimulation is added as supplementary evidence. Unfortunately, to disturb animals in this manner at each observation of apparent semitorpidity would have interfered with the experiment as a whole.

DISCUSSION

Although this study of hibernation was confined to the laboratory, it will not be inappropriate to evaluate the results in terms of a relationship which might exist between them and the natural history of *T. striatus*.

Criteria of hibernation.—As Lyman and Chatfield (1955) pointed out in their review, the word hibernation is not precise in meaning. It was for this reason that degrees of torpor were defined here. The selection of respiratory rates of 60 or 20 per minute as criteria of torpor is, indeed, somewhat arbitrary. After the experience of two years of preliminary work, however, these rates appeared to be most satisfactory, in part because it was necessary that hibernation data be quickly obtained with minimum disturbance to the experimental subject.

When factors such as body temperature or reaction to stimulation were considered with reference to the torpid animals, judgments based on respiratory rates were regularly verified. The more uncertain nature of the semitorpid state, at least at the beginning of its range, has already been indicated.

Conditions of the experiments.—The darkness and high humidity (85 per cent) of the cold room resembled conditions of a natural burrow more closely than did the unheated or warm rooms. Diffuse lighting was not a factor, however, because torpor often occurred where this was present.

Our limited observations of semitorpidity in some warm-room animals suggest a possible independence from ambient temperature for an animal with a strong tendency to hibernate. A low environmental temperature, however, strongly favors hibernation. The conditions of Series II (3°C.) seemed more favorable than those of Series I (1.5°C.). Moderate auditory disturbances perhaps hindered or shortened periods of hibernation in the unheated and warm rooms. The cold room was well soundproofed and the only disturbance there arose from inspection of animals, the animals themselves, and a fan.

Variations in behavior.—Variations in behavior explain the conflicting reports on chipmunk hibernation. In view of the fact that some individuals were awake throughout the winter, dates of earliest and latest observations for single animals above ground, so common in the literature, are not significant. References to the date when the majority of a particular population enter their burrows for the winter are of much greater value.

Mortality.—Although stress seems clearly to have caused many of the deaths, as was evidenced by post-mortem examinations, the survival percentages must be interpreted in terms of the generally accepted life span of from two to three years.

Weight patterns.—An adequate evaluation of weight cycles for a population of animals recently removed from the field is difficult because varied age groups, natural sizes, and states of health are involved. We have tried to control some of these variables by expressing the cycles in terms of percentage gain or loss with reference to an early weight, using the earliest available September weight which should be fairly stable. Perhaps an average of the first few September weights would have provided a better comparison, but it did not seem desirable to extend into the time of the experiments. Because of these variables only general conclusions may be drawn from the weight data: *T. striatus* has an annual cycle, and the average weight gains of cold-exposed animals are probably greater than corresponding gains in warm-exposed animals.

The regular pattern in many animals, reaching the same high weights at approximately the same time of the year, sometimes within a few days, is a stimulus for further investigation. The meaning of these cyclic phenomena, apparently independent of the more obvious laboratory conditions, has provoked much speculation. We will not add to these theories now, but merely indicate the challenge.

The report that *T. striatus* is lean when it enters its burrow in the fall has often been related to its extensive food storage and to speculations concerning the inability of this species to hibernate for prolonged periods. The present data suggest that this type of reasoning is in error because *T. striatus* could gain weight *after* retiring below ground. Weight cycle peaks and hibernation were encountered quite late in the laboratory, only after prolonged exposure to cold, during months when field naturalists are unlikely to capture specimens.

Periodic awakenings.—It appears that periodic awakenings are not caused by a need for food, at least at the beginning of the hibernating season, because chipmunks at that time are ordinarily obese. Perhaps, and this seems more likely to us, the awakenings are related to the chipmunks' physiological needs for water. There are, of course, many other possible factors, and so the cause remains obscure.

From the aspect of time sequence these awakenings resemble those of the hamster and differ strikingly from those of the ground squirrels, woodchucks, and some field mice, with their more lengthy torpid periods. The weight cycle of the hamster (Lyman, 1948, 1954; Panuska and Wade, 1958), however, is

quite different from that of the chipmunk, and perhaps the waking stimulus differs for each.

SUMMARY AND CONCLUSIONS

1. From September to June, numbers of eastern chipmunks, *Tamias striatus*, from Wisconsin were maintained for the purpose of studying weight patterns and hibernating habits. These animals were kept under various conditions: in a constant-temperature warm room (20°C.), in an unheated room (with varying temperature), and in a cold room (1.5°C. or 3.0°C.). Temperatures of the cold room were lowered gradually over a four-month period.

2. These experiments demonstrated that *T. striatus*, as a group, has an annual weight cycle in captivity. Cold-exposed groups showed a rise in weight of about 25 per cent from September to January and a comparable drop thereafter even if no hibernation was apparent. The average weight gains of cold-exposed animals were greater than corresponding gains of warm-exposed animals.

3. Four months of exposure to cold were ordinarily required before any hibernation occurred. The first hibernation regularly followed several weeks after the weight peak had been reached and a decline begun. This decline is perhaps indicative of a physiological change immediately preparatory to the impending lethargy. Usually a week or two of semitorpidity (respiration 20–60 per minute) preceded the first torpor (respiration below 20 per minute).

4. Although torpor was frequent, many degrees of activity occurred during the winter season. These degrees ranged from daily activity to torpor for several months, excepting periodic awakenings. During two experiments, 33 and 18 per cent, respectively, of cold-exposed animals remained active during the entire ten-month periods of exposure; 31 and 18 per cent achieved only semitorpidity. Torpor was observed in 36 and 65 per cent of the animals. The earliest torpor was on December 19, the latest on June 15.

5. Torpid animals usually awakened at least every three or four days, semitorpid animals daily. Respiration in torpid animals had a periodicity resembling Cheyne-Stokes breathing. Active cold-exposed animals had body temperatures averaging 37.6 ± 1.53°C.; active warm-exposed, 38.5 ± 1.17°C.; torpid animals, 6.0 ± 0.77°C. The semitorpid ranged between these two extremes.

6. The above results indicate that *T. striatus* has an annual weight cycle and frequently attains deep torpor which involves a low body temperature and drastically reduced respiratory rates. This species, therefore, despite its varied behavior, appears to be a somewhat deeper hibernator than has been commonly believed.

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Woodstock College, Woodstock, Maryland. Received April 15, 1958.

TWO UNUSUAL SUBFOSSIL BISON SPECIMENS FROM TEXAS

By Walter W. Dalquest

As a result of efforts of several investigators in recent years, the history of the genus *Bison* in North America has been rather well outlined. Within the boundaries of the United States, this may be summarized as follows (see Hibbard, 1955): complete absence of *Bison* during the early and middle Pleistocene; appearance of forms with gigantic horns (*latifrons, chaneyi, alleni*) in Sangamon time, and perhaps as early as Illinoian time; the replacement of these giants by smaller species (*antiquus, occidentalis*) in Wisconsin time; replacement of the latter, in turn, by the still smaller modern buffalo, *Bison bison*, of the Recent Epoch.

The several extinct species of North American *Bison* are presumed to be immigrants from Asia. Skinner and Kaisen (1947) suggest that the buffalo is not an immigrant but instead the degenerate descendent of the late Pleistocene *Bison occidentalis*. This has not been established by fossils.

Remains of extinct bisons are not uncommon in Texas and most of the species known to have ranged into the United States have been found in that state, including *Bison latifrons, B. chaneyi, B. alleni, B. antiquus* and *B. occidentalis*. Bones of *Bison bison* are locally abundant in superficial deposits over much of the state. The writer has recently obtained three specimens of *Bison* from deposits of a geologic age apparently intermediate between that of the buffalo and the latest Pleistocene *Bison antiquus* and *Bison occidentalis*. Two of these specimens are quite unusual in characters and are not typical of any described species of the genus. Both are referred to *Bison bison*, which they most closely resemble, but if they are typical of the earliest Recent representatives of that species, the thesis of Skinner and Kaisen must be abandoned.

The first specimens were discovered 9¼ miles south and ¾ miles west of the town of Electra, Wilbarger County, Texas, on April 13, 1957. Here an exposure of hard conglomerate, consisting largely of angular fragments of reworked Permian shale, and containing abundant fossils of freshwater mussels, was searched for vertebrate remains. Beaver Creek had cut through the deposit and formed cliffs 10 to 20 feet high. In a lens of silt in this conglomerate cliff, Miss Linda Dalquest found the jaw of a *Bison*. The jaw was in place and almost completely exposed by erosion. In a tiny pool below the silt lens, almost obscured by algae, were found another *Bison* jaw, a partial metacarpal, and a fragmentary scapula. All bones were blackish in color, similar in texture, and had obviously washed out of the single silt lens.

The first jaw discovered (Midwestern University No. 826) is of a young but mature animal. The stage of wear is approximately between S-1 (late adolescence) and S-2 (early maturity) on the scale of Skinner and Kaisen. Dentition is complete except that the incisors and anterior premolar are missing. The jaw and teeth are large, equal in size to the largest jaw of *Bison bison* available for comparison, but much smaller than the jaw of a *Bison alleni* found a few

miles away (Dalquest, 1957). The jaw might be referred to *Bison bison, B. antiquus* or *B. occidentalis* (Plate I).

The second jaw (M.U. 827) is from an old animal, with all teeth well worn, and approximately S-3 (full maturity) of Skinner and Kaisen. In this specimen also the dentition is complete except for the incisors and P_2. This jaw, however, and the teeth, are smaller than those of any available bison. The jaw is actually smaller than that of a Hereford heifer. No described species of *Bison* even approaches this specimen in small size. Either it represents an undescribed species or is an abnormal individual of a known species. Dwarf animals, or "runts," occur sporadically in many species and are known in several genera of bovids. The present specimen may be of this type. It is rather surprising that it should have lived to such an age under natural conditions.

Since the extreme anterior end of the jaw and the posterior-ventral portion are missing, no measurements of length of the ramus are possible. The alveolar length of the tooth row is 136 mm.; vertical depth of ramus under M_3, 42.5 mm.; width (thickness) of ramus under M_3, 31.0 mm.; least depth of diastema of ramus, 21.6 mm.

The associated metapodial is small but too incomplete for further statement. The scapula is too fragmentary to be of value.

Accurate dating of these specimens is impossible. It is not even certain that the silt lens is of the same age as the conglomerate in which it lies. The silt in the lens is very dark brown while that of the modern creek deposits is bright reddish brown. The bones are almost black in color, but when the scapula was broken it was noted that the coloration penetrates only a fraction of an inch. The underlying bone is not greatly mineralized. When a fragment of the scapula was heated to incandescence it was very slightly charred and gave off a distinct odor of burned protein. In contrast, bones of the Recent buffalo, from the prairie soil a few yards away from the conglomerate cliff, burned, charred, smoked and gave off a choking odor of burned animal matter when heated. Although obviously much older than the buffalo bones, the specimens from the silt lens are better termed subfossil than fossil. They may safely be considered latest Wisconsin or earliest Recent in age.

Another important discovery was made on June 14, 1957, when the flooding of a small creek on the Wichita Valley Farms, the property of S. J. Ellis, uncovered a partial skull and almost complete forelimb of a *Bison*. The site of this find is 2 miles north of the Big Wichita River and 6 miles west of Wichita Falls, Wichita County, Texas. The specimen was found and excavated by a farm worker before it came to the attention of Mrs. Ellis, who turned it over to the writer. Although much broken, the portions were readily reassembled to complete both horn cores, the cranium between the horn cores, and part of the occipital region (Plate II). Of the limb, all bones are present and largely complete except for the two unguli.

The remains (M.U. 993) are those of a small animal. Comparison with the jaw from Beaver Creek is not possible, but the Ellis Farm specimen appears

to have been larger. The most unusual feature of the specimen is the horn cores. These are directed somewhat posterior to the transverse axis of the skull, like the horn cores of *Bison bison* and *B. occidentalis*, but are shorter, straighter and relatively thicker than those of any reported *Bison*. In dorsal

PLATE I

Jaws of fossil and subfossil bisons from near Beaver Creek, Wilbarger County, Texas. TOP: jaw of dwarf bison referred to *Bison bison*, late Wisconsin or earliest Recent age. MIDDLE: jaw found in association with dwarf bison jaw, referable to *Bison occidentalis*, *B. antiquus* or a very large *B. bison*. BOTTOM: jaw of *Bison alleni*, presumably of Sangamon age.

aspect they are scarcely curved at all. The cores are as short as those of a small cow *Bison bison* but are thicker than those of a typical cow of any described species of *Bison*. The longitudinal flutings are deep and prominent, indicating that the animal was of considerable age.

The bones were imbedded in a deposit of pinkish clay that is exposed in an arroyo for several hundred yards and reaches a depth of at least 15 feet. Overlying deposits are prairie soils and contain abundant bones of the modern buffalo. Roots of plants had penetrated the clay and formed a mat between the clay and the older bones, but had not damaged the bones themselves. The bones were leached and light in weight but not greatly mineralized. A fragment of horn core was heated to incandescence but did not charr or give off odor. When a fragment from the interior of the ulna was heated it did not charr but did release a slight but distinct burnt protein odor. These remains also may be considered subfossil. Latest Wisconsin age is suggested.

The greatest spread of the horn cores, tip to tip, is 542 mm. Measurements of the left horn core, in millimeters, are as follows (for details of measurements and indices see Skinner and Kaisen, *op. cit.*): length on upper curve, tip to burr, 124; length on lower curve, tip to burr, 143; length, straight-line, tip to upper base at burr, 120; vertical diameter at right angle to longitudinal axis of skull, 70.0; circumference at right angle to longitudinal axis, 231; transverse diameter at right angle to longitudinal axis, 73.7; index of curvature, 117.5; index of compression, 95.0; index of proportion, 53.7.

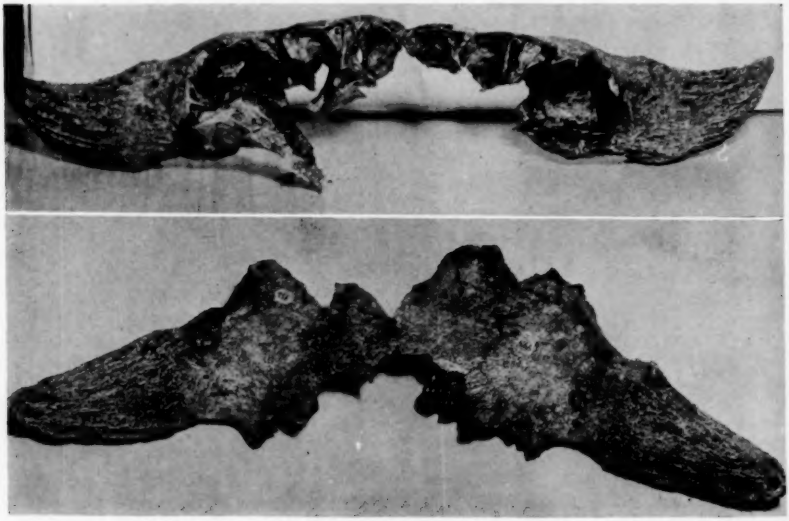

PLATE II

Horn cores of subfossil bison from near Wichita Falls, Wichita County, Texas; posterior and dorsal aspects.

No specimen of *Bison* with similar horn cores has been seen by the writer. Variation in shape of horn cores within a single species of *Bison* is considerable and it is not impossible that the Ellis Ranch specimen is simply an extreme variant of *Bison bison*—an old bull with abnormally short, straight horns.

The earliest appearance of *Bison bison* is yet to be established with certainty. If Skinner and Kaisen are correct, one would expect subfossil remains to be intermediate in size and horn core characters between *Bison occidentalis* and *Bison bison*. If the buffalo is an immigrant from Asia, subfossil remains should pertain to *Bison bison*. Of the three specimens reported here, one jaw could be referable to *Bison antiquus, B. occidentalis, B. bison*, or it could be an intergrade. Another jaw and a partial skull are so small and abnormal that they might be atypical specimens of any of the three species. An alternative suggestion, without further support, is that a small species of *Bison*, otherwise unknown, occurred in North America in latest Wisconsin time, along with *Bison occidentalis* or *Bison bison* or both. If further discoveries should support this suggestion, the later history of the genus *Bison* in North America will be more complicated than it now seems.

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Midwestern Univ., Wichita Falls, Texas. Received March 14, 1958.

COMMENTS ON THE NOMENCLATURE OF SOME MAMMALS OF THE PACIFIC NORTHWEST

BY MURRAY L. JOHNSON AND BURTON T. OSTENSON

During the past several years there have been a number of publications dealing with taxonomy of mammals of the Pacific Northwest. Many of these are detailed comprehensive studies; a few are merely short notes giving the authors' opinions, without adding to our basic knowledge. Field studies have not been correlated with most of these museum taxonomic studies, at least as related to this geographic area.

Inasmuch as our opinions are at variance with some others, we feel that a discussion and analysis may be beneficial; we do not, however, wish to give the impression that our opinions are the only correct interpretation of facts.

We hope that a properly presented challenge will stimulate further work in fields where verification is needed.

As a preliminary statement, we believe that modern taxonomic studies on the specific level and above must be based on more than simple morphologic comparisons when complex relationships are involved. The method of comparing museum skulls and skins only has its limitations in analyzing certain species; further research into their biologic nature is necessary. New concepts of the composition and dynamics of species make this broader approach virtually mandatory. However, complicated procedures in most cases of specific or subspecific determination are unnecessary. But when more extensive information becomes necessary, the total biologic relationship and not any single taxonomic criterion is important. Further, the understanding of this relationship is much more important than the name that is finally selected.

METHODS

Literature is replete with references to taxonomic methods. The following outline lists those which are either fully accepted or show promise in establishing relationships of subspecies, species and genera of mammals.

A. Classical morphologic comparisons
   1. Skin
      a. Measurements
      b. Color
      c. External characteristics of feet and other cutaneous structures
   2. Skull
      a. Size
      b. Proportions
      c. Teeth

B. Modern morphologic comparisons
   1. Baculum (Burt, 1936; Hamilton, 1946; White, 1953)
   2. Ear ossicle (Krutzsch, 1954)
   3. Hyoid bone (Sprague, 1941)
   4. Hair (Krutzsch, 1954; Nason, 1948)
   5. Genital tracts and fetal membranes (Mossman, 1953)

C. Chromosome counts and conformation (Matthey, 1952)

D. Serology and biochemical studies (Boyden, 1953)

E. Interbreeding
   1. Natural populations
   2. Laboratory populations (Dice, 1952)

F. Ecologic traits (Field studies)

G. Parasite relationships (Host specificity for parasites)

SPECIES PROBLEMS IN THE PACIFIC NORTHWEST

Peromyscus maniculatus (?) *oreas.*—Although this population of deer mice is generally regarded as a subspecies of *maniculatus*, it acts more like a species in its contacts with *P. m. austerus* in Puget Sound and with *P. m. gambeli* on the eastern slopes of the Cascades. The forms show some ecological differentiation; *oreas* is found in the deep woods whereas *austerus* and *gambeli* are taken

in more open situations. However, the forms do come in contact with each other and may even be taken in the same trap on successive nights, but we have found no evidence of integradation in these areas of contact.

In the laboratory, Liu (1954) found evidence of partial sterility between *oreas* and *Peromyscus maniculatus gracilis.*

Morphologically, *oreas* is separable from neighboring races of *maniculatus* by skull differences, such as a definitely longer rostrum, and by larger ears and a much longer tail. In addition, the greater length and different conformation of the baculum of *oreas* seem distinctive, judging from a limited series. Further information may indicate *oreas* should not be included in the species *maniculatus.*

Eutamias ruficaudus simulans.—Dalquest (1948: 259) stated that he was unable to separate specimens of *Eutamias r. simulans* and *Eutamias amoenus canicaudus* in northeastern Washington in many cases. The measurements of the two are certainly very similar. A careful comparison of standard body and skull measurements of two series of specimens of these forms shows no significant differences except for a slightly longer ear in *simulans.* But as evidence to separate these forms we find a number of differences: for example, a distinct difference in habitat preference where the two are found in the same general area. *E. r. simulans* occurs in forest cover whereas *canicaudus* is found in the more open areas. In addition there is a bell-like call note of *simulans* that may possibly be a distinguishing field character.

White (1953) shows the difference in the bacula of *E. ruficaudus simulans* and of *E. amoenus luteiventris.* Three specimens of *amoenus* (Puget Sound Museum Nos. 2563, 2829, and 2831) and three specimens of *ruficaudus* (P.S.M. 2818, 2820, and 2822) from Loon Lake, Stevens County, Washington, show differences of the same magnitude.

Thus these two species of chipmunks occurring together are readily separable when utilizing full data of field observations and bacula. Here is a situation in which two perfectly valid species occur together, yet are so closely similar as to defy differentiation by usual morphologic criteria or, at most, show differences of the degree usually associated with subspecific differentiation.

Zapus.—A similar situation exists in *Zapus* whose morphologic differences have been interpreted as those usually associated with subspecific variation. For several years *princeps* and *trinotatus* have been considered conspecific, and *hudsonius* has been separated from *princeps* with some difficulty. Krutzsch (1954), using the characters of the hair and the baculum, among others, has been able to separate this group into three apparently valid species.

Microtus.—Ellerman and Morrison-Scott (1951) have combined *Microtus agrestis* of the Old World and *Microtus pennsylvanicus* apparently because of morphologic similarities. However, Matthey (1952) shows that both the conformation and the count of the chromosomes are significantly different at the species level. Such a fundamental difference as in chromosomes must be regarded as strong evidence of species difference.

These instances cited above cast doubt on similar situations in which species are combined on morphologic grounds alone despite violation of basic biological principles. It would seem reasonable, therefore, where complete barriers exist, or where several subspecies occur in the same general locality, that more than morphologic comparison should be presented as evidence of conspecificity.

Clethrionomys.—The red-backed mice in western Washington have a complicated taxonomic history. Three forms were initially recognized from the state. In 1890, Merriam described *Evotomys occidentalis* from Aberdeen, Grays Harbor County. In 1894, Rhoads described *Evotomys pygmaeus* from the mouth of the Nisqually River in Pierce County and, in 1897, Bailey named *Evotomys nivarius* from the Olympic Mountains.

Taylor and Shaw (1929: 23) recognized *occidentalis* and *nivarius* as subspecies of *Evotomys gapperi* with *pygmaeus* placed in synonomy with *occidentalis*. After considerable field and museum experience in the state they concluded that: "The subspecies of *Evotomys gapperi* in Washington State grade into one another by scarcely perceptible degrees and it is difficult or impossible to draw a satisfactory line between them."

Hinton (1926: 216) grouped our species of red-backed mice with Old World forms although he apparently had few specimens from North America. He concluded that *E. gapperi* and *idahoensis* (among others) appear to represent the Old World *glareolus* group. On the other hand, he judged *E. occidentalis, nivarius, caurinus, mazama* and *obscurus* (among others) to be "... judging from the description, possibly more or less modified members of the *rutilus* group." And he thought that *E. californicus* and *mazama* could possibly be regarded as dwarfed representatives of the European *E. rufocanus*.

Davis (1939: 306) using the presently accepted generic name of *Clethrionomys*, considered *C. occidentalis* and *C. nivarius* to be in the *californicus* group, as distinguished from the *gapperi* group.

Dalquest (1948: 341–344) placed *nivarius* as a race of *gapperi*, and *occidentalis* as a race of *californicus*.

Hall and Cockrum (1952: 300), because of page priority of *occidentalis* over *californicus*, placed all coastal red-backed mouse populations from northern California into British Columbia, including *occidentalis, nivarius* and *caurinus*, under the species *occidentalis*.

Our collecting has been fairly extensive in western Washington. In our experience there is a continuous red-backed mouse population in the coniferous forests from the Cascade Mountains (inhabited by *C. gapperi cascadensis*) to the Pacific Ocean. In no general area or altitude studied was this species found to be absent in its preferred habitat.

Furthermore, the skins and skulls and a limited number of bacula of mice from western Washington appear to be typical of the species *gapperi*. The only well-marked group by color is a small series of seven duller and darker specimens from various localities near the ocean.

In summary, therefore, all *Clethrionomys* north of the Columbia River should

be referred to the species *gapperi* and the populations in western Oregon and northern California should be retained in the species *californicus*.

In further support of this conclusion, Cowan and Guiguet (1956: 205) state strongly their opinion that *caurinus* is a subspecies of *gapperi*; they do, however, retain *occidentalis* as a species for one specimen from British Columbia.

Long-tailed shrews of the Pacific Northwest.—Findley (1955) has analyzed the long-tailed shrews belonging to the currently recognized species of *Sorex vagrans, Sorex obscurus, Sorex pacificus* and related forms. He has attempted to clarify the relationships of this very difficult group by placing them all under *Sorex vagrans*. This treatment creates wide areas of geographic overlap of his subspecies. These occur to a large degree in areas where we have worked intensively. We find little evidence to support this departure from traditional biological principle, that is, a wide overlap in geographic range of subspecies without definite ecologic differentiation.

The evidence presented by Findley is based entirely on morphologic characters which, as we have noted, are subject to definite limitations. He has drawn heavily upon opinions stated in literature regarding parallel relationships of subspecies to one another in several genera of the Pacific Northwest. The tenuous bases of several of these have already been commented upon above.

The comparison of populations does appear to be well done by Findley and such information is certainly well worth presenting. The true biologic relationship of these *Sorex* groups, however, is still an unknown quantity and we believe this must be studied in greater detail before a final conclusion is reached. In the meantime, Jackson's (1928) classification remains workable and less confusing.

Sorex pacificus and Siberia.—A tremendous gap in the continuity of distribution of a species has here been postulated on slender evidence. In 1937, Ognev described *Sorex mirabilis* from the Ussuri region, eastern Siberia. Bobrinskii *et al.* (1944) state: "Comparing *Sorex mirabilis* with excellent photographs of skull, measurements and descriptions of *Sorex pacificus* given in H. Jackson's monograph of the American Shrews, 1928, we have been unable to find a single feature by which Ussuri shrews may with certainty be distinguished from the form *S. p. pacificus*." This was cited by Ellerman and Morrison-Scott (1951: 44), who apparently accepted this diagnosis of the situation because they write (1951: 54): "*Sorex pacificus* Coues 1877, Giant Shrew. Approximate distribution of species: Ussuri region of eastern Siberia; northwestern United States (California, Oregon)."

Thus we have a situation in which populations from different continents and thousands of miles apart are considered to be conspecific by prominent workers in two countries. We think it admirable that the morphologic realtionship is recognized, but strongly decry the taxonomic method. We question a change in name which is based on such indirect comparisons apparently without examination of specimens.

SUMMARY

A brief review of some methods of taxonomy of mammals is given. Utilizing various factors, the following basic biologic relationships are postulated: (a) The *oreas* population of *Peromyscus* behaves in many ways as a full species; pending further information it is well to consider this in the analysis of *Peromyscus maniculatus* populations of the Pacific Northwest. (b) *Eutamias amoenus canicaudus* and *Eutamias ruficaudus simulans* are races of two valid species which are grossly similar but can be definitely separated from one another by several taxonomic methods. (c) *Microtus agrestis* of the Old World and *Microtus pennsylvanicus* of North America appear to be separate species on the evidence given by reported chromosome studies. (d) The red-backed mice of western Washington all belong to the species *gapperi*, and not to the *californicus* group as suggested by recent authors. (e) The relationship of *Sorex vagrans*, *Sorex obscurus*, *Sorex pacificus* and allied forms remains too complex to be settled on the basis of simple morphologic relationships; further work and interpretation are necessary with this group before accepting any gross combination into a single species. Finally, the conspecific relationship of *Sorex pacificus* of the middle Pacific Coast and *Sorex mirabilis* of Siberia, as outlined by recent European writers, is questioned.

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OBSERVATIONS ON THE PLURAL OCCUPANCY OF POCKET GOPHER BURROW SYSTEMS

By RICHARD M. HANSEN AND RICHARD S. MILLER

Pocket gophers are solitary animals with vigorously defended territories and it is seldom that more than one gopher is trapped in the same burrow system. It is axiomatic, however, that some burrows must be occupied by more than one animal during the breeding and, since pocket gophers have not been bred in captivity and are difficult to study in the field, data from plural captures may provide valuable information about their breeding cycle, dispersal and territorial behavior.

Plural captures of *Cratogeomys castanops* (Russell, 1954), *Geomys breviceps* (English, 1932), *Thomomys bottae* (Burt, 1933; Miller, 1946), *T. townsendi* (Horn, 1923), and *T. talpoides* (Wight, 1930; Scheffer, 1938; Aldous, 1957) have been reported, but in most cases the number of gophers involved in plural captures has been too small to be of value, except to increase the list for which plural captures are known.

The purpose of this paper is to report 63 plural captures of 133 individuals in a total sample of 881 pocket gophers (*Thomomys talpoides*) from western Colorado, and to discuss the possible significance of plural captures in the life histories of pocket gophers.

METHODS

The data presented in this paper are for individuals of *Thomomys talpoides fossor* Allen trapped during the summers of 1955, 1956 and 1957 at Grand Mesa, Mesa County; Black Mesa, Gunnison County; and Deep Lake, White River National Forest, Garfield County. All three areas are plateaus at elevations of 10,200 to 11,000 feet elevation in western Colorado. The gophers were trapped in mountain meadow habitats in the spruce-fir zone.

These results were incidental to data obtained in other studies, and no attempt was made to restrict the number of traps or sets in each burrow system. In his study of the plural occupancy of burrows by Dalles pocket gophers (*T. talpoides quadratus*), Wight (1930) restricted his traps to one set in each burrow, thereby increasing the probabiilty of plural captures. His results were, therefore, a more accurate index of plural occupancy than those obtained in this study. In this study Macabee traps were set wherever signs of recent activity were found. In most cases two traps facing in opposite directions were set in each opened runway, although the number of traps per set varied from one to three in some cases. The traps were left in place for 48 hours and checked every morning and evening. Plural captures were noted by attaching a marker showing the age and sex of each animal captured to the stake to which the trap was secured. Although each burrow system undoubtedly received more than one set, plural captures were recorded only when more than one gopher was caught at the same set. These data are the results of approximately 6,000 trap-days.

RESULTS

The plural captures recorded for nine samples during the summers of 1955, 1956 and 1957 are shown in Table 1. Of the total of 881 gophers captured, 133 were involved in 63 plural captures in 10 different age-sex combinations.

Seasonal distribution of plural captures.—The seasonal distribution of plural captures is shown in Fig. 1, with the samples grouped in half-month periods according to the mean date of each sample. Since the study areas are all located above 10,000 feet elevation, they are inaccessible before mid-June and samples were not obtained before or during the start of the breeding season, which probably begins early in April. By early June, 24.4 per cent of the gophers captured were taken in plural captures. This proportion increased to 30.0 per cent during the last part of June and reached a peak of 41.7 per cent in the first half of July. Approximately 13 per cent of the animals taken in the latter part of July and the first half of August were in plural captures, and the only plural capture recorded after mid-August involved two young gophers in the September, 1956, sample from Black Mesa.

Aldous (1957) studied populations of *T. talpoides moorei* on the Wasatch Plateau in central Utah and recorded only nine plural captures of 20 individuals in a fifteen-year sample of 1,600 gophers. His study area was located at about 10,000 feet elevation in habitat comparable to Grand Mesa, Black Mesa, and

TABLE 1.—*Plural captures of pocket gophers (Thomomys talpoides) recorded at Grand Mesa, Black Mesa and Deep Lake, Colorado. Plural combinations of males (♂), females (♀) and young (y) are shown in left column opposite the number of individuals involved in each combination and the number, in parentheses, of plural captures recorded for each combination*

	GRAND MESA June 12–15, 1956	BLACK MESA June 19–22, 1956	GRAND MESA June 27–July 11, 1956	GRAND MESA July 30–31, 1957	DEEP LAKE Aug. 7–18, 1956	BLACK MESA Aug. 21–22, 1956	BLACK MESA Sept. 10–20, 1955	BLACK MESA Sept. 7–14, 1956	BLACK MESA Sept. 19–Oct. 10, 1957	Total
♂	17	8	38	30	19	3	24	31	49	219
♀	12	5	51	43	11	5	29	30	50	236
y	2	1	38	22	28	21	51	59	71	294
♀ y			36(18)	6 (3)	2(1)					44(22)
♂ y			18(9)	2(2)						20(10)
♀ ♀	2(1)	2(1)	8(4)		2(1)					14(7)
♂ ♂	2(1)	2(1)	6(3)	2(1)						12(6)
y y			8(4)		2(1)			2(1)		12(6)
♂ ♀		2(1)	6(3)	2(1)						10(5)
♂ ♀ y	3(1)	6(2)								9(3)
♂ ♀ ♀			3(1)							3(1)
♂ ♂ ♀										—
♂ y y				3(1)						3(1)
♂ ♂ y										—
♀ y y	3(1)				3(1)					6(2)
♀ ♀ y										—
Totals	41(4)	20(3)	218(34)	110(7)	67(4)	35	104	122	170	881(63)

Deep Lake; but his observations were made during July, August and September when none of the females was pregnant or in estrous and the breeding season had passed. Thus, if the plural occupancy of burrows is associated with breeding, the probability of plural captures was even less in the samples taken by Aldous than in the present study, although one might expect a greater frequency than the 1.2 per cent he recorded. However, of the nine plural captures reported by Aldous, six occurred in July, one in August and two in September, so that the seasonal trend was similar to that observed in the present study.

The highest percentage of plural captures reported was from a study of the Dalles pocket gopher (*Thomomys talpoides quadratus*) in eastern Oregon by Wight (1930). Since Wight was specifically interested in the problem of plural captures, he designed his study to record as many as possible and made only one set in each burrow. Traps were set in 288 burrow systems between March 9 and April 11, 1921, at the height of the breeding season. Fifty per cent of the burrows were occupied by more than one gopher and some contained as many as eight; in a sample of 462 gophers, 318 individuals (or 68.8 per cent) were taken in plural captures. Wight's data do not show the seasonal distribution of plural occupancy since the sample was confined to a 34-day period, but they do show that plural captures may be quite common during the breeding season, if the study is designed to demonstrate this phenomenon.

Miller (1946) recorded plural captures in February, May, July, August and December in a population of *Thomomys bottae navus* at Davis, California. Only 1.1 per cent of the total sample of 2,283 gophers were involved in plural captures, but the seasonal distribution of this phenomenon shows that it may occur at any time of the year in this species at this locality. Miller (1946) and Gunther (1956) found that reproduction occurs throughout the year in these populations and that the average adult female is capable of producing more than three litters a year. Plural captures seem, therefore, to be closely associated with breeding activity.

Age-sex combinations of plural captures.—Figure 2 shows the per cent frequency of different age-sex combinations that were recorded in the present study. These data are compared with those obtained by Wight (1930). The plural combination that occurred most frequently in Wight's samples was young with young (38.9 per cent). Adult females were taken with males in 22.7 per cent of the plural captures he recorded. This value represents approximately 46 per cent of the total sample of females, of which 52 per cent were pregnant and 47 per cent lactating. Adult males and young were taken together in 16.6 per cent and females with young in 15.7 per cent of the plural captures. Adults of the same sex were seldom captured together, and then only after an interval of several days between the first and second captures.

In the present study, females and young were the most common combination, occurring in 36.5 per cent of the plural captures. Males and young were taken together in 18.9 per cent of the plural captures, males with females in 13.5 per cent, two females in 10.8 per cent, two young in 10.8 per cent, and males

with males in 9.5 per cent of the plural captures. Thus, young gophers occurred together far less frequently, and adults of the same sex more commonly, in the Colorado samples than in Wight's study.

DISCUSSION

The burrow system of a pocket gopher constitutes both its home range and territory. Individual requirements of food and shelter are found within the burrow system and the area it occupies, and the burrow is vigorously defended against invasion by other gophers (Tryon, 1947). A rigid system of fixed territories cannot persist during the breeding season, however, and territorial behavior becomes, to some extent, subordinate to reproductive instincts. Different degrees of territoriality, or subordination of territorial behavior, imply that one animal may tolerate another to varying degrees during different phases of the breeding cycle. For example, we may outline the breeding cycle and its related events as follows: mating, pregnancy, birth of young, care of young, weaning, and dispersal of young. Adult males and females may tolerate each

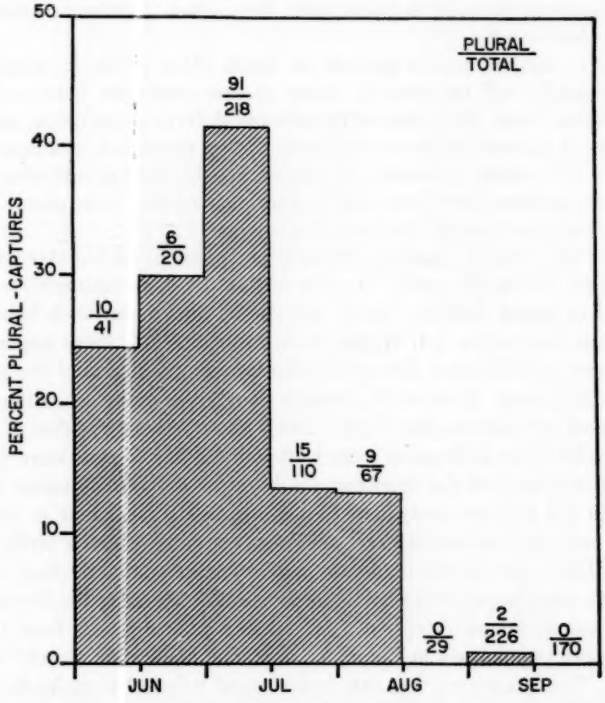

FIG. 1.—Percentage of individual pocket gophers involved in plural captures during the months of June, July, August and September.

other only during mating; both sexes may live together during the period of pregnancy; or males may be tolerated by females after the young are born, and may even share in caring for the young after they are weaned. Each of these possibilities represents a different degree of toleration and subordination of aggressive behavior.

Very little is known about the territorial and breeding behavior of pocket gophers but inferences can be drawn from the seasonal occurrence of different age-sex combinations in plural captures. A comparison between the data from this and previous studies shows a close correlation between reproductive activity and plural occupancy of burrows. The one instance of a plural capture after mid-August in the present study involved two young gophers, which presumably were in the process of establishing territories. Aldous (1957) found that multiple catches in July consisted entirely of adults, while those in September involved juveniles. He states that the peak of the mating season is over by the early part of July in that area, and that none of the females taken during September was pregnant and only a small percentage of the July females were carrying young. Further evidence is found in the fact that plural captures occur throughout the year in populations that lack a definite breeding season (Miller, 1946).

Records of marked pocket gophers on Black Mesa (Hansen, unpublished) show that adults will occasionally move to new territories between fall and spring. Ingles (1949, 1952) also noted seasonal shifts in home range, apparently in response to adverse moisture conditions during snow melt and heavy spring runoff. To this extent, territories are not permanent. At low altitudes in Colorado, where gophers have been trapped throughout the year, plural captures were only recorded during the breeding season.

Almost every possible combination of adult males, adult females and young was recorded during this study. In view of the fact that combinations of adult males and pregnant females, males and young, and males with females and young occur fairly often (cf. Wight, 1930; Aldous, 1957), there appears to be a high degree of toleration throughout the breeding season and the period of caring for the young. None of the females found with males by Adlous (1957) was pregnant or in estrous, but Wight (1930) found in his study that 47 per cent of the females taken with males were lactating and 52 per cent were pregnant. No record was kept of the breeding condition of individuals taken in plural captures in the present study, but Wight's data are sufficient to show that males are tolerated by females that are pregnant or have given birth.

Tryon (1947) has shown that male gophers come into breeding condition earlier than females and remain in breeding condition after the females have bred and are no longer receptive. The same relationship has been found in pocket gopher populations in Colorado, as is true of most seasonally breeding mammals. Tryon reasoned that this factor might induce the males to seek the females in their burrows to mate. Since males are also found in burrows with females after breeding has ceased, Aldous (1957) suggests that such cases might

also be explained by males entering female runways "on the bare chance of finding the female still receptive." Wight (1930) concurs with this explanation. As additional evidence, Wight cites the fact that he recorded only one plural capture involving two adult females and 12 plural captures of adult males. In other words, the tendency for the males to enter different burrows in search of receptive females may account for the occurrence of adult males together. In the present study, 12 plural captures of adult males and 17 plural captures of adult females were recorded. Although it is possible, and seems quite likely, that the mating phase of the breeding cycle occurs when males seek out receptive females, one must also conclude that female gophers tolerate the presence of other gophers at all stages of the breeding cycle and that they also enter the burrow systems of other gophers.

It is evident that the system of territories is considerably relaxed during the

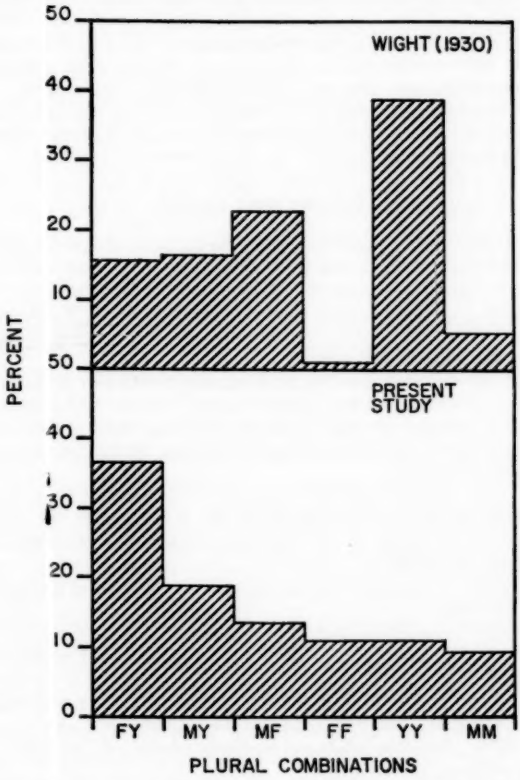

FIG. 2.—Per cent frequency of different combinations of males (M), females (F) and young (Y) in plural captures. Data reported by Wight (1930) are compared with those from the present study.

breeding season in pocket gopher populations. Whether adult males share in caring for the young after they are weaned is not certain. These data neither confirm nor deny such a conclusion. Territories apparently become re-established by September, after the young have dispersed from the parent burrows, and remain relatively stable and mutually exclusive until the next breeding season.

SUMMARY

1. Plural captures of 133 individuals in 10 age-sex combinations in a sample of 881 pocket gophers from western Colorado were analyzed and compared with similar data from previous studies.

2. The seasonal occurrence of plural captures of pocket gophers is closely correlated with breeding activity. Plural captures occur throughout the year in populations that do not have a definite breeding season.

3. Almost every possible age-sex combination of adult males, adult females and young was recorded.

4. Although it seems likely that the mating phase of the breeding cycle occurs when adult males seek out receptive females, females also tolerate other gophers at all stages of the breeding cycle and also enter the burrow systems of other gophers.

5. The system of territories is considerably relaxed during the breeding season. Territories apparently become re-established by September and remain relatively stable and mutually exclusive until the next breeding season.

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THE MAMMALS OF PALM VALLEY, FLORIDA

By R. DeWitt Ivey

A portion of the northeastern coast of Florida, in St. Johns County and bounded roughly by the towns of Ponte Vedra, Vilano Beach and Palm Valley, was studied intermittently by the writer over the years 1939–1956. While its spectacular array of dunes, virgin coastal forests and palmy islands deserves perpetuation, this region is rapidly falling to the bulldozer and the dredge. The notes summarized herein attempt to describe the habitat preferences of some of the mammals and to place on record a list of mammals reported from the Palm Valley area. Other local studies on mammals of northeastern Florida have been made by Allen (1871), Bangs (1898), Harper (1927), Moore (1946, 1949) and Pournelle and Barrington (1953). The present paper deals more extensively with coastal environments than do any of the earlier papers, and is presented in the belief that opportunities to study undisturbed coastal regions of this type are apt to diminish or disappear.

In connection with this study, I am indebted to the University of Florida for a grant and for equipment, to H. B. Sherman for direction, assistance and encouragement, to A. M. Laessle and I. J. Cantrall for assistance and criticism, to the Florida Game and Fresh Water Fish Commission for permits, and to residents of Palm Valley, including Eston Barkoskie, Merlyn Mickler, and E. B. DeGrove for information and help on various occasions of difficulty.

The Palm Valley region occupies the southern half of a barrier island which, in its original state, was split cleanly away from the mainland by salt marshes and channels in its upper quarter and lower half. Just above the middle, however, it was only partially separated from the mainland by a hardwood swamp and scattered freshwater marshes. Since 1910 a canal of the Intracoastal Waterway system has made the area a true island.

From the air this region has a striated appearance owing to the adjustment of plants and watercourses to the many narrow and parallel bars, dunes, terraces and lagoons left above sea level by an earlier receding shoreline. Highest elevations occur on the eastern side of the island, especially along the active dune ridge which varies from about 20 to 50 feet above sea level. Considering such a narrow range of altitude, the variations in vegetation, water level and soil due to altitude are striking. The ecological picture, already involved with the meeting of inland, subtropical and coastal elements, is further complicated by these edaphic variations and by the extensive and narrow interdigitation of most of the communities.

For the sake of brevity, detailed descriptions of the plant communities will be avoided in this paper. The plant names used are those of Small (1933). The work of Kurz (1942) was of help in analysis of dune communities. The principal biological communities investigated are as follows: (1) *Beach* and *dunes*, including chiefly such divisions as *bare sand*, mixed *vanguard vegetation*, sparse to dense stands of *sea oat* (*Uniola paniculata*), damp *swales*, and *scrub* con-

sisting of thickets of live oak (*Quercus geminata*) and saw palmetto (*Serenoa repens*); (2) *Hammock* which has been described by Laessle (1942) as "a broadleaved, evergreen forest," characterized by a rich variety of plants dominated by laurel oak (*Quercus laurifolia*), live oak (*Q. virginiana*), magnolia (*Magnolia grandiflora*) and cabbage palm (*Sabal palmetto*); (3) *Hardwood swamp*, a semi-aquatic or damp-ground forest characterized by white bay (*Magnolia virginiana*) and tupelo gum (*Nyssa biflora*); (4) *Cypress swamp*, an aquatic forest dominated by pond cypress (*Taxodium ascendens*); (5) *Flatwoods*, the low, coastal plain pineland dominated by loblolly pine (*Pinus taeda*) and slash pine (*P. palustris*), with an understory of saw palmetto and other plants; (6) *Salt marshes*, consisting of pure stands of marsh grass (*Spartina alterniflora*) or black rush (*Juncus roemerianus*); (7) *Natural islands* with vegetation consisting of small segments of mainland communities; (8) *Dredge deposit islands*, with vegetation representing early seral stages; (9) *Freshwater marshes* characterized by open pools, marsh grass (*Spartina bakeri*) and an encircling belt of saw palmetto.

Mammal records were obtained by live-trapping with Sherman traps, by snap and steel traps, by investigation of nests and burrows, from road kills, from information supplied by local residents, and from sight records. In the following accounts, the phylogenetic order and scientific names are those of Miller and Kellogg (1955). Common names are those most used by observers in this area. Where not substantiated by specimens, subspecific identification is presumed from existing range maps.

ACCOUNTS OF SPECIES

Didelphis marsupialis pigra Bangs. Opossum.—Fourteen records were obtained, including 11 specimens observed and tracks from three additional localities. Opossums were found to be widely distributed, occurring in nearly all habitats. Records were distributed as follows: dunes, 2; dune-scrub margin, 3; hammock, 3; hammock-salt marsh margin, 1; freshwater marsh, 3; salt marsh island, 2; flatwoods, 1. Opossum tracks were not as abundant as raccoon tracks, but the number found dead on roads was much greater. A female and seven *Peromyscus*-sized young were found dead on March 22, 1940. On February 5, 1947, a set of small tracks measuring 1 inch in length was found with those of an adult. The skull of a large opossum (greatest length: 135 mm.) was found under the nest of a bald eagle.

Blarina brevicauda carolinensis (Bachman). Carolina short-tailed shrew.—One specimen was taken by a rotting pine stump, in a hammock, 50 feet from a freshwater marsh.

Cryptotis floridana (Merriam). Florida short-tailed shrew.—Two specimens were taken on small, treeless islands in the salt marsh, under dense grass, just above the narrow, damp beach.

Scalopus aquaticus australis (Chapman). Mole.—Two specimens were obtained from hammock areas, but tunnels were observed in dunes, scrub and flatwoods. Networks of mole tunnels were especially common under logs.

Lasiurus borealis seminolus (Rhoads). Seminole bat.—A specimen was shot on July 27, 1956, among flatwoods pines, near a hammock margin. Bats of the same appearance were fairly common.

Dasypterus floridanus Miller. Florida yellow bat.—Two specimens of this large, pale species were obtained on July 4, 1953, and July 28, 1956, from beach and dune areas where it appears to be the most common bat. It appears especially to hunt the pockets of

dead air in the back-dune depressions, where mosquitos and flies are abundant, as well as to cruise and cross the entire beach and dune area. It was not observed to be an especially high-flying species, as reported by others, except when in transit from one feeding locality to another.

Dasypus novemcinctus mexicanus Peters. Armadillo.—Armadillos entered the Palm Valley area only during the latter portion of this study. Eston Barkoskie, a Palm Valley resident, reported seeing his first armadillo about 1946. Since that time they have become familiar animals, and the writer has observed a road kill, burrows, and tracks in hammock, marshy hammock border, and flatwoods ditch bottom.

Sylvilagus f. floridanus (J. A. Allen). Eastern cottontail.—Although no specimens were obtained, sight records of this species, and scats, tracks and runways probably belonging to it, were noted in dunes, hammocks and flatwoods. The species appeared to be more common during 1939–42 than in 1946–47.

Sylvilagus p. palustris (Bachman). Marsh rabbit.—Sight records and signs of the marsh rabbit were noted especially in the salt marshes, wherever slight elevations, ridges or islands occurred. They were observed most frequently in the dense growths of *Spartina* bordering such areas. They were also seen at the edges of freshwater marshes surrounded by hammock and by flatwoods. When pursued, they readily swim the marsh waterways. A good colony was found on a small grassy island, less than an acre in area, surrounded on all sides by permanent water channels over 150 feet in width.

Sciurus c. carolinensis Gmelin. Gray squirrel.—These were distributed throughout the Palm Valley hammocks, judging by nests, sight records, and specimens obtained. They are often seen in the higher hammocks which contain old pines and hickories, and are at least as common in the low hammocks, where they may be heard for a great distance clashing the resonant fronds of the cabbage palms. They seem especially drawn to the water edges where hammocks meet fresh or salt marshes. E. B. DeGrove reported a hawk striking in mid-air a squirrel which he had just shot out of a tree. On another occasion an owl covered a squirrel just after it had fallen to the ground. The writer frequently observed Cooper's hawks in the vicinity of gray squirrels, and one was seen swooping and diving for some time among trees containing squirrels.

Among the gray squirrels of Palm Valley, as elsewhere in Florida, there is considerable variety in coloration. Specimens were obtained which had a distinctly reddish or rusty coat, while others were of the more common olive-brown color.

Sciurus niger shermani Moore. Fox squirrel.—Residents reported having shot fox squirrels in Booth Hammock in the 1946–47 hunting season. At that time, adjacent to Booth Hammock, there was a stand of tall, old pines, more closely resembling inland fox squirrel habitat than any other spot in the region. It is possible that a small population lived in this forest until its destruction by logging in 1947. No records were obtained by the writer, and in general the region does not appear to be hospitable to fox squirrels.

Glaucomys volans querceti (Bangs). Southern flying squirrel.—These little squirrels, though seldom seen, are characteristic of the hammocks in the Palm Valley region. By means of headlights, flying squirrels were observed climbing, gliding and eating acorns in several of the hammocks. Some were flushed from hollow tree dens, which may generally be recognized by the superfluous strands or mats of Spanish moss issuing from the entrances. S. A. Grimes, of Jacksonville, has told me that an abundance of Spanish moss is characteristic of flying squirrel nests. Others were driven from outside nests, which were rather common.

This type of nest, which has been described by Moore (1946), somewhat resembles that of the golden mouse, but differs in several respects. Those observed in Palm Valley were roughly spherical, about 6 inches in diameter, and had one conspicuous opening. They were composed largely of black Spanish moss fiber and twigs woven together, with an inner lining of shredded grasses and bark. They were usually found in a rather secure location such as a crotch or among finger-sized branches of a small oak tree. The height of

these nests is usually greater than that of golden mouse nests, being 10 or 15 feet. Nests are used by individuals or families. The outside nests are most abundant near hammock edges, where the forest roof slopes downward to meet the adjoining scrub.

Oryzomys palustris (Harlan). Rice rat.—Specimens were taken in several of the moister habitats, as follows: Back-dune hammock, 1; freshwater marshes, 5; salt marsh and small islands, 11. In the salt marshes rice rats were commonly found nesting under pieces of driftwood or in hollow palm logs in 1940–42, during a period of abundance. The nests were placed on ground which was firm and elevated just above the high tide level. The nests were made of the common marsh grasses and rushes. In protected bays of the salt marsh and in freshwater marshes nests were commonly placed in standing grass at heights varying from ground or water level to 2 feet above the water. The nests were spherical, about 4 or 5 inches in diameter, and were composed of a coarse outer layer of shredded grass blades and stems compactly woven together, with an inner lining of the same material more finely shredded.

A pregnant female containing four 3–4 mm. embryos was taken on October 27, 1946. On May 1, 1941, several families of rice rats were discovered under driftwood with young varying in age from newborn to about two weeks.

Peromyscus polionotus phasma Bangs. Anastasia Island beach mouse.—As reported in a previous paper (1949) this specialized mouse appears to be confined to the dune habitats, and principally to the sea-oat growth and adjacent bare sand areas. Its range in general conforms to the 25–500 foot wide strip of dunes facing the ocean. Pournelle and Barrington (1953), on Anastasia Island, took this species in scrub areas as far as 1800 feet from the dunes. Since scrub is often, if not basically, a dune community, this should not be too surprising, although trapping in such areas failed to take any specimens in the Palm Valley area.

These mice are not as white as the sand, or as the west Florida beach mice. This does not seem to be due to any interbreeding with inland forms, but more likely to the time element. In this connection, it appears probable to the writer that the evolution of concealing coloration in these and other types of beach mice should proceed with more directness and speed because of the prevailing wind and the noise of the ocean surf. The combined effect of wind and surf would be to eliminate sound and scent, and to place a premium on visual methods of predation.

Peromyscus g. gossypinus (LeConte). Cotton mouse.—This is the common wood mouse of the area, with its center of abundance clearly in the hardwood hammocks. It is also common in flatwoods, hardwood swamps, and was also taken in dunes, scrub, freshwater marsh and dredge deposit island. In the hammocks and drier swamps it far outstrips its associates the golden mouse, shrews and woodrat. In the flatwoods it is about the equal of the cotton rat. Its numbers appeared to be markedly lower in 1946–47 than in 1939–42, in general agreement with several other small species.

Peromyscus nuttalli aureolus (Audubon and Bachman). Golden mouse.—Golden mice were found to be characteristic of the hardwood forests, including all types of hammocks and the hardwood swamps. Their distribution is discontinuous and can be traced by locating the arboreal nests, as pointed out previously (1949).

Sigmodon h. hispidus Say and Ord. Cotton rat.—In 1946–47 specimens were taken in various habitats, as follows: back-dune hammock, 1; palmetto thicket bordering freshwater marsh, 4; salt marsh islands, 5; marsh beach at hammock edge, 2; flatwoods, 1. They were taken in most damp communities, largely avoiding the wetter *Oryzomys* habitats, and the higher hammocks, scrub and dunes.

The above records were secured by roughly 2,000 trap-nights in cotton rat habitat, during a low period in their abundance. In July, 1956, 19 specimens were taken in 75 trap-nights in a flatwoods area, and four were taken in 25 trap-nights in a freshwater marsh edge. Their short, shallow tunnels were abundant in the damp ground of both habitats. They appeared to be unable or totally disinclined to climb trees or bushes even when hotly pursued.

Neotoma f. floridana (Ord). Florida wood rat.—Specimens and stick houses observed indicate that the wood rat belongs to the hammocks and drier hardwood swamps. It is certainly more common in the hammocks immediately behind the dunes than in more inland woods, while most other mainland species exhibit the reverse tendency. Its houses and well-beaten trails are especially abundant on the very back slope of the dunes, where this is shaded by hammock trees. The excessive ground litter in this wind-whipped forest appears to be much to their liking, as their buildings flourish out of materials immediately at hand.

The houses observed were usually made of hardwood sticks about ¼ to ½ inch in diameter, larger but lighter pieces of palm petioles, and pieces of palm leaf resembling half-closed Japanese fans. These were accumulated in a large pile about 1 to 3 feet high and 4 or 5 feet in diameter. One to three main tunnels led into the nests from the edge of the pile. Considerable burrowing and excavating was generally done under the pile of sticks, so that the floor of the nesting chamber was of clean, freshly turned soil, and the nests were somewhat below the level of the ground. The nests were made of rather coarsely shredded palmetto fiber, and as in the case of the golden mouse, cotton trap markers were quickly appropriated for the nest lining. On one occasion what appeared to be a regular latrine was found about a yard from the stick house, with a well-beaten path leading to it from one of the main entrances. It consisted of a patch of ground about 10 inches in diameter, almost solidly covered with droppings.

Variations included houses built around hollow logs, or sloping up the side of a standing trunk. A young specimen was taken from a hollow live oak, sticks having been used to fill the cavity up to about 5 feet from the ground. In a hardwood swamp a large accumulation of debris containing a woodrat nest was found suspended about 5 feet from the ground in a dense tangle of vines. Another house was built in an old dredging pipe about 18 inches in diameter.

A one-third grown young was taken in early April, 1940, and a one-fourth grown young (38 grams) was taken on January 3, 1947.

Mus musculus brevirostris Waterhouse. House mouse.—One specimen was taken beside a burrow on a small dune surrounded by a damp swale located in the back dunes.

Tursiops truncatus (Montagne). Bottle-nosed porpoise.—A stranded specimen and many sight records showed this species to be a regular inhabitant of the coastal waters and the salt marsh channels. On September 3, 1946, from a distance of 15 feet, the writer observed two porpoises engaged in what appeared to be a mating procedure. The larger individual was crowding the other into shallow water near a marsh beach so that the bodies of the animals were only about two-thirds submerged. This activity continued for about half an hour. In the inlet near St. Augustine, porpoises were observed feeding. Fishes of 10–15 inches appeared sometimes to jump, and again to be thrown end over end into the air. The porpoises repeatedly leaped and caught the fish in mid-air at heights varying from 3 to 10 feet.

Urocyon cinereoargenteus floridanus Rhoads. Gray fox.—Various residents reported having seen or killed foxes. Fox tracks were observed on a canal beach near a mixed marsh and swamp area.

Euarctos americanus floridanus (Merriam). Black bear.—Bears are regularly hunted in the extensive swamps just west of Palm Valley. In this area, the writer observed tracks, beds, claw marks and droppings. This forest contains many large, hollow trees and logs up to 6 feet in diameter which probably serve as dens for these animals. Numerous newspaper accounts, with dates, weights and photographs, indicate that these bears run rather large—one, for example, weighing 672 pounds. In one account, four cows and six hogs were said to have been killed by bears.

Procyon lotor elucus Bangs. Raccoon.—Seven specimens, 23 sight records, and numerous tracks showed the raccoon to be present in every major habitat. Its center of abundance, however, appears to be the wetter hammocks, swamps and marshes. The adjustment of

raccoons to tides has been discussed by the writer in a previous paper (1948). Raccoon populations increased markedly from 1939 to 1947. This opinion is based on the numbers of sight records and signs, and the results of actual traplines run by the writer or by professional trappers during this period.

Mustela frenata olivacea A. H. Howell. Long-tailed weasel.—Merlyn Mickler, a resident of Palm Valley, reported having taken one weasel in many years of trapping.

Mustela vison lutensis (Bangs). Mink.—No mink records were obtained by the writer or by Palm Valley trappers, although Eston Barkoskie said that the Minorcan inhabitants of Anastasia Island, just to the south, trapped mink in the salt marsh using wooden box traps made to float on the tide. Bangs (1898) reported them to be abundant and easily caught in the marsh a few miles north of here.

Mephitis mephitis elongata Bangs. *Skunk.*—A road kill in a scrub area just behind the dunes provided the only specimen of this species. Residents reported the presence of skunks near their houses.

Lutra canadensis vaga (Bangs). River otter.—Various residents reported having seen and trapped otters in the numerous freshwater ponds and marshes.

Felis concolor coryi Bangs. Florida panther.—Perhaps no animal would testify so convincingly to the primeval character of these coastal forests as the panther. It should be remembered that vast, uninhabited marsh and swamp areas extend north and south of Palm Valley and on the west meet the extensive river swamps of the St. Johns, and that until recently wild horses inhabited the salt marshes. The animal is definitely claimed for the area by local residents, and details of a panther hunt were described by Eston Barkoskie.

Lynx rufus floridanus Rafinesque. Bobcat.—Tracks were seen on the beach of a marsh island, and Merlyn Mickler reported having taken them "fairly often in coon traps." An adult and three kittens were reported for December 23, 1946, by Eston Barkoskie.

Trichecus manatus latirostris Harlan. Manatee.—Various residents reported having seen manatees in the salt marsh channels. They are said to feed commonly around the docks at St. Augustine, just south of Palm Valley.

Odocoileus virginianus seminolus Goldman and Kellogg. White-tailed deer.—Deer are hunted in the vicinity, but mainly to the west of the Palm Valley area. Residents reported rare instances of deer in the areas closer to the coast.

Domestic animals.—Ecologically, it would be impossible to describe the mammals of Palm Valley without paying considerable attention to the cattle which graze the flatwoods and marshes and trip through the hardwood forests as silently as deer; or the feral pigs which must be harvested with guns and dogs by local residents who inhabit small clearings in the hammocks; or the herds of wild horses or "marsh tackies" which apparently have only recently been exterminated. Space does not permit a thorough discussion of these inhabitants.

SUMMARY

Mammal investigations reported herein were conducted in the vicinity of Palm Valley, St. Johns County, Florida, from 1939 to 1956. The distribution of mammals in nine major and several minor habitats is discussed. Thirty-four species of mammals are listed as occurring in the area, although ten of these were not collected or seen by the writer.

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OBSERVATION OF NOCTURNAL ANIMALS BY RED LIGHT

BY ROBERT B. FINLEY, JR.

Red illumination has the great advantage that it does not dazzle the eyes of an observer or of subject animals. In 1948 I tried watching nocturnal animals at the University of Kansas Natural History Reservation. Different light sources and filters were tried. The method was used at several localities in Colorado as part of a study of the distribution and ecology of the wood rats (Finley, 1958). The purpose of this report is to describe the method, to give results that show the behavior and responses of some mammals to red light, and to urge others to use red light observation as an aid for studying the behavior of nocturnal animals.

The difficulty of making direct observations at night in undisturbed conditions has greatly handicapped the study of nocturnal animals. White light has been successfully used by many observers, but few kinds of mammals will carry on undisturbed activities under white light. Southern *et al.* (1946) tried using infra-red equipment known as the "sniperscope," developed in World War II. They had some success with the brown rat (*Rattus norvegicus*) attracted to bait indoors, but the equipment was inconvenient to carry any distance for watching wild animals. More recently, Southern (1955) has reported using visual red light with good results in a study of predation by the tawny owl (*Strix aluco*) on the wood mouse (*Apodemus sylvaticus*).

EQUIPMENT AND METHODS

The simplest and most effective light filter was a disc of red acetate sheet such as is sold in some photo stores for darkroom safelights. Such a disc cut to the proper size was inserted under the lens of a three-cell flashlight. A somewhat wider beam and greater range were obtained by using a Delta lantern with a 6-volt dry battery, such as is commonly sold for camping. A deep red nail polish can be painted on the glass in place of the red acetate filter.

Because of the low light intensity and narrow field of vision, the beam sometimes must be moved rapidly to keep the animal in view. The motion of the light source induces distracting shadow motions that sometimes cause loss of contact with the animal. A useful improvement is a portable floodlight powered by an automobile storage battery to provide a fixed illumination of a wider field of view.

In a situation where an extension could be run from a 110-volt electrical outlet, general illumination with red light bulbs might give best results. The animals could then be preconditioned by burning the lights continuously for one or more nights before attempting to observe.

For writing field notes at night I found it convenient to carry a small pen-type pocket light which was coated with red nail polish.

PHYSIOLOGICAL BASIS OF NIGHT OBSERVATION

A comprehensive explanation of the nocturnal and diurnal vision of many kinds of vertebrates has been presented by Walls (1942). A general understanding of the visual adaptation is essential in making most effective use of artificial light.

The adaptations of special significance involve the photoreceptor cells of the retina, which consist of two general kinds, the rod cells and the cone cells. Although the retinas of most kinds of vertebrates contain both kinds of receptors, the rods are especially abundant in predominantly nocturnal animals, whereas the cones are especially abundant and well-developed in diurnal animals.

Rods produce a deep red visual pigment called visual purple or rhodopsin, which gradually accumulates in the cell during the process of dark adaptation. When the fully dark-adapted retina is exposed to white light the rhodopsin absorbs radiant energy and is transformed to a colorless substance that stimulates the underlying nerve cells. Visual purple owes its color to the fact that deep red light is reflected by this pigment, rather than absorbed. Hence, only light having shorter wave lengths than red can be absorbed and trigger a stimulus of the optic nerve.

Cones, however, do not depend on visual purple to transmit the light stimulus but use different pigments adapted primarily for daylight vision, including the full range of the visual spectrum.

Man, like many other vertebrates, has a retina highly adapted for day vision, particularly in the center of the field, but with fair night vision in the peripheral zone of the retina. Those animals that are strongly nocturnal have predominantly or even entirely rod retinas that lack the central area of cones. It is evident that the red light can be invisible only to those kinds of animals that totally lack cones. In practice, it seems that most kinds of mammals other than bats do have some cones and may see the red light; but the low stimulus is far less disturbing than white light.

Although a man cannot hope to compete with a cat or an owl in seeing at night, he can see in a tremendous range of light intensities. When human rods are fully dark-adapted they are 100,000 times more sensitive than they are in daylight, and they can detect light at 1/5000 of the intensity at which cones go blind (Anonymous, 1944). With his eyes fully dark-adapted, which requires about 30 minutes, an observer can see surprisingly well even on a moonless night; but exposure to only a few seconds of dazzling light can undo most of the adaptation. It is therefore essential to avoid every ray of white light if one wishes to gain maximum visual advantage over the animals he is watching.

NIGHT OBSERVATIONS

While employing red light primarily to study the behavior of wood rats, I had incidental opportunities to observe several other kinds of mammals, including the wood mouse (*Peromyscus leucopus*), deer mouse (*P. maniculatus*), snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), beaver (*Castor canadensis*), and striped skunk (*Mephitis mephitis*).

Peromyscus leucopus.—At the University of Kansas Natural History Reservation, Douglas County, Kansas, I watched baited live traps on 6 June 1948 set along a limestone ledge outcrop. At 10:05 PM I saw a wood mouse stealing bait from a live trap. I "froze" where I stood while the mouse, undisturbed, made repeated trips to and from the trap, sometimes entering it to take barley and sunflower seeds off the treadle. The mouse seemed unaware of the red light for several minutes. Then it looked toward me a few times and, as though curious, approached cautiously and climbed up a slender branch to within about 4 feet of the flashlight. The mouse stared into the beam toward me for a few moments, then turned and scampered back toward the trap. It returned again to stare at me but, at 10:25, I changed my stance and rustled a twig. This alarmed the mouse; it turned and scampered down the branch and disappeared up the trunk of an elm tree.

On 5 July 1951, near the same site, I saw three or more *Peromyscus* stealing rolled-oat bait from two live traps. One mouse made five trips in rapid succession into a trap; it avoided springing the trap each time by hopping over the trigger crossbar. Twice that evening two mice came swiftly around opposite ends of the trap and ran headlong into each other. In each case they just dashed on after the momentary stop and showed no hostile reaction. They seemed to ignore each other's presence.

Peromyscus maniculatus.—Three miles north of Almont, Colorado, at 8300 feet elevation, I caught an adult female deer mouse in a trap set in a vertical cleft of a low sandstone cliff. The following evening I released the mouse shortly after midnight, on 23 July 1949. When the trap was opened the mouse acted cold and hungry. She ignored me and paid no attention to the red lights. She nosed and dug in the loose sandy soil, threw dirt back under her body with her forepaws and kicked it out behind with her hind feet. She uncovered a sunflower seed, gnawed open the shell, and ate the seed. She seemed to find seeds directly by sense of smell before digging. Finally, she closed her eyes and apparently went to sleep. Not only did this mouse seem oblivious to the red lights, but her senses and fear seemed generally to have been dulled by hunger and cold.

Lepus americanus.—On the night of 13 July 1949 I observed two snowshoe hares at the Gold King Mill, 8 miles north and 1 mile west of Hesperus, 9500 feet, Colorado. I had entered a two-room shack and seated myself on a small trunk just inside the door. At 9:25 PM I was abruptly startled by a snowshoe hare that made a loud "thump" on the floor and scrambled noisily into the bedroom. It had evidently hopped into the room without either of us being aware of the other. I scanned the room with the red flashlight, and in the far corner saw the rabbit. Presently, a second snowshoe hare bolted across the main room and stopped at my side. It sniffed alertly, but showed no awareness of the red beam shining down on it. It hopped swiftly across the bedroom into the far corner, and during the next few minutes both hopped slowly around the room. I continued my observations of the two hares until 10:03, both inside and outside the cabin.

Neotoma cinerea.—A subadult female was observed foraging on the night of 21 July 1949, 3 miles north of Almont, Colorado. She had been trapped the previous night, and was calm and docile, showing little fear of man. She was released at the place of capture at 10:26 PM, and emerged from the trap toward a red floodlight placed only 4 feet away. She began avidly eating leaves of mountain sage (*Artemisia frigida*), ignoring the red flood light and my presence only 6 feet away. After eating for a few moments the rat ran along the slope searching for food. She ate ravenously, sometimes stripping most of the leaves off herb stalks, sometimes nibbling only part of a leaf before hurrying on. She ate leaves and tender stems of at least ten species of plants, but not every kind encountered. Plants

eaten were *Populus tremuloides, Artemisia pacifica, Chrysothamnus parryi, Chenopodium, Oenothera coronopifolia, Eriogonum cernuum, Chrysopsis villosa* and *Cryptantha fendleri.* This young rat was followed for an hour and 25 minutes, during which she was recaptured and released a second time.

Other mammals.—Many hours of observation of the Florida wood rat (*Neotoma floridana*) in eastern Kansas were moderately successful, though hampered by dense vegetation. Wood rats were observed foraging, grooming, and traveling back and forth over habitual routes between dens and feeding places. They were usually undisturbed by the red light but shy of moonlight and easily frightened by sounds.

A porcupine was watched in a shack at the Gold King Mill, La Plata County, Colorado, on a July night. It seemed to be alarmed by the red light as well as by my presence.

In October I observed beavers by red light and by white light in the La Plata River, Colorado. They paid no attention to the red light but moved about over such distances that the red light was too weak to keep them in view. White light was more satisfactory and hardly more disturbing.

At Two Buttes, Colorado, I saw a striped skunk take refuge in a small culvert at night in May. It was wary and remained in the culvert for 25 minutes. The skunk seemed to be as much disturbed by red light as by white light.

The red-light method should have much value for studying nocturnal rodents, predation and nesting habits of owls, and roosting activities of bats. It may be useful for studying some kinds of nocturnal fur-bearers, such as foxes, mink and bobcats. Although the degree of nocturnal adaptation of an animal's eyes may indicate the possibility of using red light to advantage, only actual trials will determine whether the method can be successfully employed against a particular kind of wildlife.

SUMMARY

Night observations of wood rats and other nocturnal animals were tried with the aid of visual red light. Satisfactory results were obtained by use of very simple equipment. Eight species of mammals were observed with varying degrees of success. Best results were obtained with the bushy-tailed wood rat and the snowshoe hare in Colorado. Young individuals are easiest to watch because they are less wary of strange sounds and intruders.

Under favorable conditions, red-light observation is a valuable method for study of the behavior of nocturnal animals. It is a direct means of getting information not available in any other way.

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ZYGODACTYLY IN THE MEADOW MOUSE

By Frank B. Golley and Theodore F. Whitmoyer

Fusion of the digits of vertebrates has interested biologists, particularly human geneticists, for a long time. Although this condition has been reported in many mammals, it has not, so far as known, been observed in the genus *Microtus*. In this paper we wish to report on (1) the discovery of fused digits in a wild meadow mouse, *Microtus P. pennsylvanicus* Ord, (2) our subsequent experiments designed to determine the inheritance of the trait and (3) the characteristic expression of the trait in offspring resulting from crossing studies.

Fusion of the digits may be caused by (1) a fusion of the phalangeal bones or (2) the presence of a skin web between two separate phalanges. Weidenreich (1922) suggested that the term "zygodactyly" be used when a skin web occurred between the third and fourth digits of the forefeet and the second and third of the hind feet, and that "syndactyly" be used for all other conditions of digital fusion. We are concerned only with zygodactyly in this paper. Apparently zygodactyly is due to the persistence of the interdigital webbing which is present in the embryo and in the newly born *Microtus*. Usually this webbing disappears, but with a local arrest in the normal development of the fore and hind feet, a zygodactyl condition may result.

Zygodactyly is fairly widespread throughout the higher vertebrates. It is the normal condition in some marsupials (Diprotodontia; Morrison, 1946), primates (some Lemuridae, Catarrhinae, siamang apes and gorillas; Straus, 1926) and rodents (*Castor, Myocastor, Ondatra* and *Hydromys*; Straus, 1926), and has been regarded generally as an adaptation to an aquatic or arboreal existance. Of the microtine rodents, only the muskrat (*Ondatra zibethica*) has webbing between the toes of the hind feet. In the meadow mouse, zygodactyly is not normal, there being four separate digits on the forefeet and five on the hind feet. The first digits on the forefeet are normally absent.

The meadow mouse is a terrestrial mammal living in communities where grasses and herbs provide sufficient food and cover. Moist or boggy conditions provide optimum habitat, but it is also commonly observed in dry, upland fields. It may swim readily (Blair, 1939; Low, 1944) but, as far as is known, it does not climb trees.

In the fall of 1955, Don W. Hayne captured an adult, male meadow mouse which exhibited a complete skin web between digits 2 and 3 on both hind feet. This animal was live-trapped in a grass field on the Michigan State University campus and was brought into the laboratory with other meadow mice for a study of growth rate (Whitmoyer, 1956). All observations on zygodactyly were made on this male or its offspring.

METHODS

The fore and hind limbs of five zygodactyl mice were placed in nitric acid to dissolve away the soft tissues. In this way it was possible to show that

the bones were not fused and that the condition was zygodactyly, as defined by Weidenreich (1922).

The mice were maintained in the animal laboratory of the Department of Zoology, Michigan State University. White-enameled sinks were used as breeding cages, with artificial light supplied in excess of 15 hours. Water was provided at all times. The mice bred and gained weight satisfactorily on a ration of lettuce, carrots and oatmeal. Wood chips were furnished for bedding and metal houses provided cover.

The original zygodactyl male was mated with 12 normal wild females to obtain young for the growth-rate study. Some of these offspring were zygodactyls and these were backcrossed to the original male. Alternately, some F_1 matings were made among the zygodactyl offspring. In addition, some unrelated zygodactyls were mated and there was one backcross of a normal female from a zygodactyl cross with a zygodactyl male.

When parturition occurred, the number of young born was recorded. About the tenth day the fore and hind feet became fully developed and the presence or absence of zygodactyly could be determined.

TABLE 1.—*Records of crossing experiments; zygodactyls indicated by underlining*

CROSS		NO. OF CROSSES	NO. YOUNG BORN	NO. YOUNG DYING 1–10 DAYS	NO. WITH TRAIT	PER CENT ZYGODACTYL	
						Of total born	Of live young
Unrelated	♀ × ♂	19	71	31	17	23	41
Unrelated	♀ × ♂	3	8	0	6	75	75
F_1	♀ × ♂	5	17	2	7	41	47
Backcross	♀ × ♂	2	6	0	3	50	50
Backcross	♀ × ♂	1	1	0	0	0	0

RESULTS

An analysis of the crosses made during the investigation (Table 1) indicated that zygodactyly may be inherited in the population as an autosomal dominant. In the first cross, assuming that the wild females were homozygous normal and the male was heterozygous for the trait, we would expect 50 per cent of the offspring to be zygodactyls. The observed frequency of zygodactyly in those offspring reaching an age when the trait was evident was 41 per cent. The difference between the observed and expected frequencies was not significant (Chi-square value of 1.62). The sex ratio of both zygodactyl and normal offspring was approximately 50 : 50.

It was necessary to terminate the experiment before sufficient F_1 and backcrosses could be made to determine if the hypothesis of autosomal dominance was correct. In the F_1 crosses a 1 : 1 ratio was observed rather than the expected 3 : 1 ratio. Since we would expect that a 1 : 1 ratio would occur in approximately 25 per cent of the crosses, the observed frequency does not disprove

the hypothesis of autosomal dominance. In the even more limited data from the unrelated zygodactyl matings the expected 3 : 1 ratio was observed. Although these data do not disprove the hypothesis, additional crosses are necessary before it can be accepted without reservation.

Straus (1926) and other workers, in their analyses of human pedigrees, have shown that webbed digits in most cases appear to be inherited as Mendelian dominants, but in others may be sex-linked dominants or recessives. Several interruptions of the breeding schedule interfered with attempts to build pedigrees for the mouse population.

The characteristic expression of zygodactyly in *Microtus pennsylvanicus* is shown in Table 2. The trait appears with almost equal frequency in males and females. Although the condition appeared most frequently on the hind feet (30 per cent), it was not unusual to find webbing on all feet (24 per cent). In only 3 per cent of the mice was webbing confined to the forefeet. Further, in most cases fusion was complete and extended to the end of the digits. The incidence of partial webbing may be somewhat higher than shown in Table 2 (6 per cent), since in very young animals the webbing may have broken before the initial examination. In most cases of complete fusion the skin web persisted throughout adult life.

TABLE 2.—*Character of zygodactyly in males and females*

CHARACTER	NUMBER			
	Male	Female	Unknown Sex	Total
In all fore and hind feet	3	3	2	8
Both hind feet	3	5	0	8
Both front feet	0	0	1	1
Slight webbing hind feet	2	0	0	2
Trait in both hind and one fore	2	0	0	2
Unknown character	0	0	12	12
Totals	10	8	15	33

It was also interesting to note that the survival rate of young born of the zygodactyl × normal and zygodactyl × zygodactyl crosses was fairly low. A total of 103 young were born; of these, 33 died before 13 days of life, resulting in a survival rate of 68 per cent. This rate can be compared with the 78 per cent survival of normal × normal crosses made by Whitmoyer (1956).

When several adult male *Microtus* were caged together a fight generally ensued during which one or more males were often badly injured or killed. Observations of aggresive behavior of normal and zygodactyl mice indicated that zygodactyl males were less successful in combat than were normal males. Possibly the condition of webbed digits is a disadvantage to a male in combat or, alternately, inbreeding (to four generations in the laboratory) may have reduced the stamina and fighting ability of the zygodactyls.

During the breeding experiments a "silver" or "gray" mutation was observed

in one mouse. A cross between two zygodactyl animals (third generation) produced three young; one of these exhibited the zygodactyl condition on all four feet and an unusual grizzled pelage in which the white hairs were predominant. The mixture of white and brown hair gave the animal a silver or gray appearance. The silver pelage was not continuous over the entire body, but was particularly pronounced on the back and over the chest. The color of this mouse did not correspond clearly with any of the aberrations discussed by Owens and Shackelford (1942) and Clarke (1938). One other young of this cross showed webbing on the hind feet; the remaining young mouse died soon after birth.

DISCUSSION

The unusual characters occasionally observed in wild mice, color aberrations and, in this case, zygodactyly, apparently arise by mutations. It might be expected that these mutations would become evident particularly in a small isolated population, which presumably has a high incidence of inbreeding. In the present instance, the area in which the original wild male was captured was surrounded on two sides by roads, on one side by a large dirt pile, and on the fourth side by a closely clipped pasture. This population could probably be considered as, at least, semi-isolated.

After the trait of zygodactyly was recognized in one male, a careful examination was made of all *Microtus* captured in live and snap traps in population studies in the same field where the male was taken and in other areas studied by Golley (1958). In all, over 700 animals were captured in the vicinity of East Lansing and none of these showed any evidence of webbing between the digits. Since workers studying small mammal populations with live traps often clip toes as a marking technique, it would be expected that zygodactyly, if at all common, would have been recognized and described in the literature. To our knowledge, this has not been the case. The variety of foot configurations and digit shapes and sizes observed in wild *Microtus* lead us to suggest that these characters may be less rigorously selected by the environment than are characters of other body structures. However, our experiments and observations in the laboratory indicate that in the present instance, at least, fusion of the digits may be a disadvantage to the individual in fighting activities, and to the population in a lower survival rate. Possibly these two factors favor the disappearance of zygodactyly arising in a wild population through mutation.

It is also interesting to speculate on the value of zygodactyly to the meadow mouse. In marsupials zygo- or syndactyly is believed to be of advantage in hair combing or cleaning (Muller, 1930; Morrison, 1946) and in climbing (Sera, 1940). In the primates webbing between the digits may be of value in an arboreal habitat (Weidenreich, 1923). Furthermore, in various rodents, moles and shrews webbed feet are an adaptation to an aquatic environment. As mentioned earlier, *Microtus* may live in a marshy or boggy habitat and may swim readily. Might not webbing between the digits allow this mammal to make further use of this semiaquatic environment?

Finally, it is suggested that unusual, easily observed genetic characters in small mammals, such as zygodactyly, might be useful in studying the problems of genetic drift in mammal populations. For instance, establishment of a population with a high incidence of zygodactyly, followed by continued live trapping in this central and in adjacent populations would give information on the drift of zygodactyly out of and its dilution within the central population.

SUMMARY

Zygodactyly, or fusion of the second and third digits by a skin web, was discovered in a wild male *Microtus*. This animal was mated to normal wild females and various crosses were made among the offspring of these initial crosses. From limited data, it is suggested tentatively that the condition of zygodactyly was inherited as an autosomal dominant. Fusion was observed only between digits 2 and 3 of the hind feet and digits 3 and 4 of the forefeet. Fusion was most commonly observed on the hind feet alone (30 per cent of those exhibiting the condition). Various speculations are made regarding (1) the incidence of an unusual condition, such as zygodactyly, arising in a population, (2) the advantage of webbed feet to the meadow mouse, and (3) the use of zygodactyly as a genetic marker.

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DENTAL PATTERNS IN *PEROMYSCUS* OF FLORIDA

By Robert S. Bader

An analysis of the accessory dental structures in 17 species of *Peromyscus* was made by Hooper (Misc. Publ. Mus. Zool., Univ. Mich., 99: 1–59, 1957). Only one of the four species of *Peromyscus* found in Florida, *P. nuttalli*, was included in the study. Data pertaining to the other species (*P. floridanus*, *P. gossypinus* and *P. polionotus*) was obtained by the author in the course of a study involving Pleistocene representatives of the genus found near Reddick, Marion County, Florida.

Hooper found considerable variation in the frequencies of the accessory dental structures (lophs and styles) within a given dentition as well as within and between species populations. In general the incidence of the lophs and styles was greater on the first than on the second molar and greater on the labial than on the lingual side of the tooth. The M_2 and the lingual side of the uppers exhibited the lowest frequencies. Most of the present data agree well with these generalizations (Table 1).

Although variation in the dental patterns was quite properly emphasized by Hooper, it should be noted that the frequency of several dental features may be essentially fixed at 0 or 100 per cent in many species. Of the 16 traits studied, 7 in *P. floridanus*, 8 in *P. gossypinus* and 4 in *P. polionotus* show a frequency greater than 95 per cent or less than 5 per cent. Most of these are in the uppers. In *P. nuttalli*, one of the least variable species of the genus in this respect, 13 of the 16 characters are essentially invariable.

Only data concerning penetrance, i.e., the percentage of individuals exhibiting a trait, are presented. Expressivity, i.e., the degree to which a trait is expressed, may also vary considerably as shown by Hooper. Although these were recorded for the three species, they are not included in the present report.

Geographic distribution.—The geographic distribution of the samples was as follows: *P. floridanus*—Highlands Co., 51; Alachua Co., 22; Levy Co., 18; Putnam Co., 3; St. Johns Co., 2. *P. gossypinus*—Putnam Co., 17; Levy Co., 15; Highlands Co., 13; Collier Co., 8; Brevard Co., 6; Alachua Co., 5; Marion Co., 2; Palm Beach Co., 2; DeSoto Co., 1; St. Johns Co., 1. *P. polionotus*—Marion Co., 25; Alachua Co., 13; St. Johns Co., 7; Highlands Co., 5; Escambia Co., 3; Levy Co., 2; Indian River Co., 1; Brevard Co., 1; Okaloosa Co., 1.

To facilitate comparisons the distinctions between lophs and styles employed by Hooper were used. Approximately equal numbers of males and females are included in each sample. Only teeth of the right side were examined. The samples of *P. gossypinus* and *P. polionotus* include individuals of several described subspecies.

P. floridanus.—This form possesses the simplest dental pattern of the four species found in Florida. The pattern is comparable in simplicity to that of *P. melanophrys*. The entoloph, ectolophid, entostyle and ectostylid (except on the M_1) are rare or completely absent. The ectostylid shows varying degrees

TABLE 1.—*Penetrance of dental traits in three species of Peromyscus, expressed as a percentage;* ms = *mesostyle or mesostylid;* ml = *mesoloph or mesolophid;* es = *entostyle or ectostylid;* el = *entoloph or ectolophid;* N = *sample size*

TOOTH	MS	ML	ES	EL
		P. floridanus, N = 101		
M^1	30	100	0	0
M^2	42	84	0	0
M_1	62	55	44	13
M_2	30	4	11	2
		P. gossypinus, N = 70		
M^1	100	100	24	0
M^2	100	100	26	0
M_1	99	37	83	49
M_2	93	4	60	16
		P. polionotus, N = 58		
M^1	93	90	7	0
M^2	100	83	3	0
M_1	60	74	72	9
M_2	64	7	74	2

of fusion with the posterior face of the protoconid. For this reason, it is not always easy to determine whether this protuberance is present or not.

The most distinctive dental feature of the species is the mesoloph. This wedge-shaped loph originates at the crest of the mure and passes into the floor of the enamel valley, typically at a point about one-third the distance to the labial border. In the M^1 it often fuses at one or more points with the metacone. In the M^2 it is more symmetrically placed with respect to the valley separating the paracone and the metacone. The mesolophid, when present, is usually developed only as a slight bulge in the mure wall.

P. gossypinus.—The frequencies of the several auxiliary dental features in this species are, in general, somewhat higher than those in its close relative to the north, *P. leucopus.* It is most comparable to the Virginia population of the latter species, as analyzed by Hooper. Although similar in size, the teeth of *gossypinus* and *nuttalli* may be readily distinguished on qualitative grounds. The disparity in frequency of the accessory structures between these two species is greatest in the mesolophid and ectolophid, both being considerably less common in *gossypinus.*

The mesostyle, mesostylid and mesoloph were present in all, or nearly all, of the specimens examined. The mesoloph arises characteristically from the mure while the mesolophid and ectolophid originate from the entoconid and hypoconid, respectively. As in *floridanus,* the lingual structures of the lowers are somewhat more common than those on the labial side.

P. polionotus.—The lophs and styles of this form are quite distinctive and, therefore, more easily determined than in the other Florida species. The incidences, in general, are somewhat lower than in *gossypinus* but higher than

in *floridanus*. Comparison with *P. maniculatus*, presumably its closest relative, is difficult because of the geographic variation in that species as emphasized by Hooper. The frequencies in *polionotus* are somewhat higher than the average in *maniculatus*, particularly with respect to the mesostylid and ectostylid.

The mesoloph may arise from the mure or the posterior face of the paracone. The mesolophid typically extends lingually as a low ridge from the anterior face of the entoconid. The ectostylid, frequently tilted at an angle to the long axis of the tooth, may lie, unattached to adjacent structures, at the mouth of the valley or be fused at its base to the protoconid.

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WATER INTAKE IN THE DEER MOUSE

By Olwen Williams

It is well established (Howell and Gersh, 1935; Schmidt-Nielsen *et al.*, 1948) that the heteromyids, *Dipodomys* and *Perognathus*, can live on dry foods with no free water because of their ability to conserve the water of metabolism. In contrast, *Neotoma*, a cricetid, has much greater need for water and must get it by eating succulent food if it is not otherwise obtainable. As early as 1922 Dice reported that, under laboratory conditions of dry air and temperature of 21°C., *Peromyscus maniculatus bairdi*, the prairie deer mouse, also a cricetid, drank from 1.14 to 3.78 cc. of water per day. Later, Ross (1930) found that various species of deer mice using nest boxes drank averages of 2.16 to 4.08 cc. per day at 22 to 23°C., and Chew (1951) reported that *P. leucopus*, the white-footed mouse, drank 5.36 cc. at 17.8°C. and a relative humidity of 62.5 per cent.

Along the eastern slope of the Colorado Front Range the deer mouse occupies a wide variety of habitats, but its highest population levels appear to be attained on rocky sites sparsely covered with shrubs and herbaceous plants (Williams, 1955*a*). In the Colorado montane forests these places constitute the early successional communities that normally develop after fire, logging or similar disturbances have destroyed the existing vegetation; in the foothills they are the shrub communities that form an ecotone between forest and

grassland. During late summer and early fall, the time at which the deer mouse population reaches an annual maximum, most of these situations are hot and dry. Because the initial study of the food habits of these mice (Williams, 1955*b*) indicated that dry seeds constituted a major portion of their diet while only a small amount of green vegetation or succulent food was eaten, the present study was undertaken to determine the need of the deer mouse for free water.

Intermittently from October 1953 to March 1955 records were kept of the water freely consumed by a total of 108 deer mice. The animals observed were subadult or mature, first or second generation, offspring of field-caught mice that had been trapped in the vicinity of Boulder, Colorado, during the summer of 1953. Presumably these mice were intergrades between *P. maniculatus osgoodi* and *P. m. rufinus*; the geographic ranges of these two subspecies are contiguous along the eastern edge of the Front Range. The laboratory population was maintained during the period of study by a grant from the Council on Research and Creative Writing of the University of Colorado.

Methods.—The procedure employed to find the water consumption of each mouse was as follows: The mouse was removed from a standard stock cage, and its weight and sex determined and recorded. The animal was then placed in a small (8 × 8 × 12 in.), individual, test cage equipped with a food container and a calibrated drinking tube. No nest box was provided, but the floor of the cage was covered with a layer of clean dry sawdust. The drinking tube, purchased from the Denver Fire Clay Company, was one in which access to the water was through an opening into a small well at the bottom of the tube. The device was calibrated after purchase to record accurately changes in level to 0.5 cc. This particular type of drinking tube was used because its construction assured the constant availability of water. The amount of water lost by evaporation was determined from a filled tube kept in an empty cage under conditions otherwise comparable to those in the occupied cages.

The test cages stood side by side on two shelves in an animal room in which, from October 1953 to May 1954, a large battery of aquaria was also maintained. Evaporation of water from these tanks kept the relatively humidity in the room at about 70 to 80 per cent, while the temperature varied from 68 to 72°F. The aquaria were under constant illumination; hence the mice were subject to round-the-clock lighting, albeit of low intensity at night. Under these conditions the water intake of 26 mice was successfully measured. During the summer of 1954 the aquaria were removed. In the months that followed, the relative humidity averaged from 10 to 20 per cent and the temperature fluctuated from 64 to 72°F. The room was no longer illuminated at night. This is mentioned because it may have affected the activity patterns of the animals, although this was not observed. During this second period the water consumption of an additional 82 animals was recorded.

In the first observation period, the water in the drinking tubes was replenished daily. Later it was found that replenishing the water only as needed gave results

of greater accuracy. Water consumption was recorded on a weekly basis and the average quantity consumed per day was calculated from these data. Because the weights of the animals varied, water consumption was calculated not only as the number of cubic centimeters consumed per day per individual but also as the number of cubic centimeters consumed per day per gram of body weight. In a number of cases the water was contaminated by feces or sawdust, invalidating the results. This constituted the major disadvantage of the type of drinking device used for the tests and accounted for the limited number of records obtained.

In the first observation period (1953–1954) all the mice were fed exclusively on air-dry Purina Laboratory Chow, the available assay of which showed that it contained not more than 23 per cent crude protein. In the second period (1954–1955), the diets were varied to determine the effect that the protein content of the food might have on the amount of water drunk by the mice; hence, 28 mice were kept on air-dry Purina Chow, 26 animals were fed solely on solvent-extracted soybean oil meal with a guaranteed minimum protein content of 44 per cent, while 28 others were placed on a diet of crude barley with a protein content of only 8 per cent. As the second series of observations proceeded, differences in water consumption did appear in relation to the protein content of the food. To determine whether or not the differences would persist, a number of animals were placed on diets of either soybean meal or barley, and their water consumption was recorded continuously for a period of five consecutive weeks.

Results.—The observations made during the course of this study are summarized in Table 1. No distinction is made between males and females because no differences in water consumption appeared that could be correlated with sex.

Discussion.—Considerable individual variation in the amount of water drunk was apparent in all instances, but individual animals were consistent in their day-to-day consumpton. For example, the amount of water drunk by individuals fed on Purina Chow varied from 8.2 cc. per day to as little as 1.14 cc. per day and averaged 3.2 and 4.3 cc. under conditions of high and low humidity respectively. Howell and Gersh (*op. cit.*) and Chew (*op. cit.*) reported similar observations, but the individual variations recorded in the present study were not as great as those reported by Chew who found that at 28°C. the range in water consumption was from 3.19 to 19.11 cc. per day. He noted, however, less variation at 18°C. which was closer to the temperature under which the present observations were made. Individual differences in behavior and activity patterns may have been in part responsible for these variations. The mice that drank more than average amounts of water were highly active, doing a good deal of stereotyped somersaulting or running in the test cages.

Possibly the most interesting observations were those involving the differences in the water consumption of the animals fed on barley and soybean meal for five weeks. The validity of these results may be open to question because these were relatively natural foods and differed in more than merely protein

TABLE 1.—*Water consumption by deer mice fed on air-dry food under varying conditions*

NO. OF MICE	MEAN WGT., GM.	REL. HUMID., %	FOOD	NO. WEEKS ON DIET	MEAN DAILY WATER CONSUMPTION		
					Total cc.	cc./gm. wgt.	S.D.
			Under high and low relative humidity:				
26	21.0	70–80	Chow	–	3.2	0.16	±0.05
28	17.6	10–20	Chow	–	4.3	0.25	±0.08
			Under low relative humidity:				
28	16.7	10–20	Barley	–	3.0	0.18	±0.06
28	17.6	10–20	Chow	–	4.3	0.25	±0.08
26	16.4	10–20	Soybean	–	4.9	0.28	±0.09
			Under low relative humidity for 5 consecutive weeks:				
13	—	10–20	Barley	1	2.5	0.14	±0.02
14	—	10–20	Soybean	1	6.0	0.32	±0.14
11	—	10–20	Barley	2	2.6	0.14	±0.03
13	—	10–20	Soybean	2	6.5	0.34	±0.12
10	—	10–20	Barley	3	4.8	0.27	±0.11
12	—	10–20	Soybean	3	9.3	0.54	±0.26
11	—	10–20	Barley	4	4.3	0.28	±0.11
11	—	10–20	Soybean	4	8.4	0.46	±0.21
13	—	10–20	Barley	5	3.7	0.22	±0.10
13	—	10–20	Soybean	5	4.6	0.27	±0.25

content, but at least the observations may suggest the influence of this item in the diet. The differences in the mean daily water consumption for these two groups were statistically significant for the first three weeks of the observation period but not for the last two. When mice were first shifted from Purina Chow to barley, their amount of water freely drunk fell off perceptibly, but by the end of the fifth week on this diet the animals were drinking close to the average amounts of water for mice on Purina Chow. Likewise, the mice placed on soybean meal at first drank greater than the average amounts of water consumed by mice on Purina Chow, but by the end of the fifth week their daily water consumption was again close to this figure. Presumably the mice underwent some sort of physiological adjustment immediately following the drastic change in the protein content of their diet. The nature of this adjustment constitutes a problem for further investigation. Recently, Avrick (1956) reported that in *Peromyscus maniculatus osgoodi* the glomerular filtration rate was low compared with results obtained for related forms, and that it was not appreciably affected by alteration of dietary protein. She suggested that the mice may have kidney tubules which can excrete urea, but her work did little to elucidate the nature of the adjustment apparently made by the mice in the present study.

Schmidt-Nielsen *et al.* (*op. cit.*) reported evidence that the kangaroo rat selected food high in carbohydrates during periods of stress with respect to water, thus reducing the nitrogenous wastes to be excreted and securing more metabolic water. If the decreased need for water following a shift to a high

carbohydrate diet does not persist in the deer mouse, possibly one should question the validity of the assumption that we have long made. We have assumed that the adaptability with respect to both its food and water requirements constitutes the major factor in the success of *Peromyscus maniculatus* in inhabiting a diversity of habitats, particularly the dry, rocky slopes in the montane forest of Colorado.

SUMMARY

From October 1953 to March 1955, the *ad libitum* consumption of water was recorded intermittently for a number of deer mice. For animals fed air-dry Purina Chow, the daily water intake averaged 3.2 cc. under conditions of high relative humidity and 4.3 cc. under low. Alteration of dietary protein influenced the quantity of water drunk. The daily intake decreased or increased with a corresponding decrease or increase in protein consumption, but this difference did not persist for more than a few weeks.

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GENERAL NOTES

MAMMAL REMAINS FROM OWL PELLETS IN ARIZONA

There are now 27 Arizona records of the gray shrew, *Notiosorex crawfordi*; nine come from owl pellets (Lange: Soricidae of Arizona. Amer. Midl. Nat., 61: 96–108, 1959). Six gray shrew remains were recovered from about 75 long-eared owl (*Asio otus*) pellets collected in the spring of 1956 in scattered localities at the edge of the oaks on the south slope of the Dragoon Mountains in Cochise County (with 212 *Perognathus*, 33 *Onychomys*, 24 *Dipodomys*, 24 *Peromyscus*, 4 *Reithrodontomys*, 2 *Thomomys*, 1 *Neotoma albigula*, and 1 fringillid). One *Notiosorex* was recovered from about 50 barn owl (*Tyto alba*) pellets collected in a 35-foot shaft in desert-shrub habitat at 4,200 feet on the north side of the Santa Catalina Mountains in Pinal County (with 30 *Perognathus*, 25 *Neotoma albigula*, 8 *Peromyscus*, 6 *Onychomys*, 5 *Thomomys bottae*, and 2 *Sigmodon hispidus*). Gray shrews have also been taken from pellets, probably horned owl (*Bubo virginianus*), collected along the dry bed of the Santa Cruz River south of Tucson in Pima County (with *Sigmodon hispidus, Dipodomys, Perognathus, Peromyscus*, and *Reithrodontomys*).

About 50 barn owl pellets were collected on July 19, 1957, at the bottom of a low hill along Silverbell Road in Tucson, Arizona, one mile north of the Silverbell–Grant Road junction. Remains of 103 mammals were recovered from these pellets; pocket gophers (*Thomomys bottae*) contributed 73.8 per cent (remains of 76 individuals). Also represented were 12 *Perognathus*, 9 *Mus musculus*, 3 *Sigmodon hispidus*, 1 *Dipodomys*, 1 *Peromyscus*, and 1 *Onychomys*. Studies indicate that the barn owl has a large hunting range—about 165 acres in Davis, California (Evans and Emlen, Condor, 49: 3–9, 1947). A range of this size for the Tucson barn owls would include extensive cultivated fields, alfalfa fields, cemeteries and the beds and banks of intermittent streams where pocket gophers are numerous. Nocturnal wanderings, perhaps mainly by young *Thomomys* in search of burrow sites, and considerable surface activity after dusk on spring evenings may account for this high representation of a fossorial mammal in the diet of a nocturnal bird of prey.

C. Roger Hungerford and Joseph T. Bagnara, Jr., Department of Zoology, University of Arizona, informed us of some owl localities, and Lewis Wayne Walker, Arizona-Sonora Desert Museum, supplied us with climbing equipment.—KENNETH I. LANGE, *c/o U.S. National Museum, Washington 25, D.C., and* JOHN R. MIKITA, *1925 Santa Rosa, Tucson, Arizona.* *Received September 3, 1958.*

THE DISTRIBUTION OF SOME SMALL MAMMALS IN EASTERN INTERIOR ALASKA

There is a general paucity of information on the occurrence of small mammals throughout Alaska, and the distribution in many instances is substantiated by rather few records. During the 1956 and 1957 field seasons, many small mammals were taken at the several locations visited in conjunction with a general ecological survey of eastern interior Alaska. Some of these records serve to fill in questionable areas in the present postulated distribution of the various species of small mammals, and in two cases appreciably extend the known ranges of the species concerned. Table 1 shows the locations visited and the species of small mammals that were taken at each location; the table shows only the mammals taken and is not to be considered a list of the mammals present.

Microtus pennsylvanicus was taken from three locations beyond the present recorded range of the species; 22 specimens were collected at Black River, six at Old John Lake, and two at Small Lake (see Table 1 for exact locations). Hall and Cockrum (Univ. Kansas Publ., Mus. Nat. Hist., 5 (27): 407, 1953) show the northern limit of the range of *M. pennsylvanicus* in this area to be approximately 100 miles to the south of Old John Lake.

One specimen of *Microsorex hoyi* was collected at Small Lake. Burt and Grossenheider (A Field Guide to the Mammals, Houghton Mifflin, 1952) show the northern limit of the range of *M. hoyi* in this area to be in the vicinity of the Yukon River approximately 60 miles to the south of Small Lake.

TABLE 1.—*The locations visited during the study and the species of small mammals taken at each*

SPECIES	STEESE HIGHWAY (65°27'N, 145°32'W)	BLACK RIVER (64°44'N, 143°48'W)	SMALL LAKE (67°22'N, 143°48'W)	OLD JOHN LAKE (68°03'N, 145°W)	MT. FAIRPLAY (63°40'N, 142°10'W)	BIG DELTA PLOT NO. 3 (64°05'N, 145°25'W)	BIG DELTA PLOT NO. 4 (64°40'N, 144°15'W)	BIG DELTA PLOT NO. 6 (64°35'N, 144°55'W)	BIG DELTA PLOT NO. 11 (64°25'N, 145°20'W)	BIG DELTA PLOT NO. 13 (64°05'N, 145°25'W)	EAGLE PLOT NO. 28 (64°50'N, 143°25'W)	EAGLE PLOT NO. 29 (64°45'N, 143°20'W)	LIVENGOOD PLOT NO. 10 (65°05'N, 147°45'W)	LOBO LAKE (68°22'N, 143°55'W)	LAST LAKE (68°35'N, 143°45'W)
Clethrionomys rutilus	X	X	X	X	X	X	X	X	X	X	X	X	X	—	X
Microtus oeconomus	X	X	X	X	X	X	—	X	—	—	X	X	X	—	X
M. pennsylvanicus	—	X*	X*	X*	—	—	X	—	—	X	—	—	X	—	—
M. longicaudus	—	—	—	—	—	—	—	—	X	—	X	—	—	—	—
M. xanthognathus	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—
M. miurus	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—
Sorex cinereus	—	X	X	X	X	—	X	X	—	X	—	—	X	X	X
S. obscurus	—	—	—	—	—	—	X	—	—	X	—	—	—	—	—
S. tundrensis	—	X	—	—	—	—	—	X	—	—	—	—	—	—	—
Microsorex hoyi	—	—	X*	—	—	—	—	—	—	X	—	—	—	—	—
Synaptomys borealis	—	X	X	—	—	—	X	X	X	X	—	—	—	—	—
Tamiasciurus hudsonicus	X	X	X	—	—	X	—	—	X	—	—	—	—	—	—
Ochotona collaris	X	—	—	—	—	—	—	—	—	—	—	—	—	—	X
Citellus undulatus	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—
Lemmus trimucronatus	—	X	X	X	—	—	X	X	X	—	X	X	—	—	X

* Extensions of the recorded range of the species; see text.

In addition to these records, the writer and others have observed the hoary marmot, *Marmota marmota caligata*, on Victoria Mountain (65°47′N, 146°55′W) and they have been observed on Mt. Schwatka (65°53′N, 147°15′W) further to the west by Jack Gross (*viva voca*). The range of the marmot within the Tanana Hills is depicted by Rausch (Arctic, 6: 120, 1953) as those areas above a continuous contour of 2,000 feet. These two localities are separated from the continuous 2,000 foot contour of the Tanana Hills and White Mountains by Beaver Creek and are, therefore, not included by Rausch.

It was also noted during the field work that the ground squirrel, *Citellus undulatus*, appeared to be absent from the Tanana Hills; no evidence of it was observed at Eagle and Twelve-mile Summits on the Steese Highway, Mt. Fairplay, plot locations Eagle Nos. 28 and 29, or Big Delta Nos. 3, 4, 6 and 11. The range of the subspecies *C. u. plesius* is reported by Rausch (*op. cit.*: 122, 123) to extend from the Alaska Range well into the Tanana Hills to about the vicinity of the Steese Highway; this range is questionable and this subspecies probably does not range north of the Tanana River in this area.

All specimens taken during the study have been incorporated into the University of Alaska Museum collection.—WILBUR L. LIBBY, *Alaska Dept. of Fish and Game, Fur and Game Division, Box 105, College, Alaska.* *Received June 2, 1958.*

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SOREX ARCTICUS AT MAUGERVILLE, NEW BRUNSWICK

Austin W. Cameron (Jour. Mamm., 39: 292, 1958) indicates doubt about the identification of a specimen of *Sorex arcticus* collected by P. Cox at Maugerville, Sunbury County, New Brunswick, as recorded under the name *Sorex richardsoni* by Cox (Bull. Nat. Hist. Soc., N. B., 14: 53–55, 1896). During my studies of American long-tailed shrews I examined two imperfect dry alcoholic specimens of this species collected by Dr. Philip Cox and in the collection of the Miramichi Natural History Society, Chatham, New Brunswick. I suspected at that time that these specimens might represent an undescribed subspecies, and passed it with the comment: "The imperfect specimens examined from New Brunswick . . . are provisionally referred to *S. a. arcticus* rather than to *laricorum*" (Jackson, N. A. Fauna No. 51: 70, July, 1928). My view now is that the New Brunswick specimens should be referred to *S. a. maritimensis*.—HARTLEY H. T. JACKSON, *U.S. Fish and Wildlife Service, Washington, D.C.* *Received September 3, 1958.*

NOTES ON A BABY FREE-TAILED BAT

During recent studies on the free-tailed bat, *Tadarida braziliensis mexicana* (Saussure), it was necessary to send live bats from Texas to Baltimore, Maryland. Among a group of bats obtained by Richard B. Davis at Davis Cave, Llano County, Texas, on June 11, 1958, and received in Baltimore on June 12, was one pregnant female. She was separated from the rest of the bats and placed in a small cage with water. Between 6:00 and 11:00 PM that evening she gave birth to a female baby. Although the birthing was not observed, it probably occurred breech first as in *T. b. cynocephala* (Sherman, Jour. Mamm., 18: 176–187, 1937). Subsequent observations on other *T. b. mexicana* births indicate this to be the case.

The pink "hairless" baby was discovered hanging upside down with a moist placenta attached. Since the time at which the placenta and umbilical cord drops off may serve as an index as to the age of the baby, the weights given for June 12 and 14 were with the placenta and cord attached. The measurements and weight that follow were those taken at the discovery of the young bat: weight 2.7 gms., length of forearm 1.8 cm., length of fifth finger 1.8 cm., length from head to tip of tail 6.0 cm., length from head to base of tail

4.1 cm., length of thumb .6 cm., and wing span about 10–11 cm. The upper and lower canines and incisors had erupted.

An attempt was made to keep the baby alive by placing other lactating females in the same cage with the mother and young bat, as it is suspected that promiscuous feeding occurs in this species. In addition to this, warm milk, light cream, and vitamin supplements were given by means of a pipette. None of the adult females was ever observed to nurse the young bat. (Later observations of caged *Tadarida* show that baby bats, at least sometimes, will nurse on females other than their mothers.)

By the morning of June 13 the placenta had dried out considerably and the baby was squeaking and moving about well. The weight was still 2.7 gms. on June 14 but, since the placenta was well dried, a weight increase is indicated. By evening, two days after birth, the placenta and cord had dropped off. Weights on June 16 and 18 were 2.9 gms. and 2.8 gms. On the morning of June 20 the baby was found dead (2.7 gms.), possibly due to overcooling as the temperature on the previous night was unusually low. Weight and external measurements were again taken, but no significant changes had occurred. Organ wet weights (in mg.) were taken on two Roller Smith balances, 500 mg. and 25 mg. capacity: right ovary .7, left .4; right adrenal 1.5, left 1.7; right kidney 18.8, left 18.3; spleen 10.4; liver 102.0; heart 29.8; right lung 25.8, left 24.2. It should be noted that already a size difference that exists in the adults can be noted in the ovaries, the right being larger. This appears to be characteristic of the species (Sherman, *op. cit.*). Also, the left adrenal is situated on the side of the left kidney distal to the mid-line and is more elongate than the right adrenal which sits on the anterior dorsal end of the right kidney. The left kidney is somewhat more posterior in position than the right. Measurements of the intestine and stomach were 12.0 and .7 cm. The body hair was just beginning to become apparent, giving a velvet appearance to the skin at the time of death.

This work was supported by a grant from the National Institute of Health and directed by David E. Davis.—Clyde F. Herreid II, *Division of Vertebrate Ecology, School of Hygiene and Public Health, Johns Hopkins Univ.* *Received July 14, 1958.*

HOME RANGE AND ACTIVITY PATTERN OF AN ARCTIC GROUND SQUIRREL

During a barren-ground caribou survey in 1958 we were camped close to the center of the home range of a male Arctic ground squirrel, *Citellus parryi parryi* (Richardson). Our tent was only 50 feet from his main den. From June 11 until July 5 we observed this mammal almost daily. He became very accustomed to us and lost all fright. Therefore we could follow him regularly to his various dens. Between these dens he traveled in an almost straight line. Figure 1 shows the home range, estimated to be 10 acres. The location of various dens, and the den where a pregnant female was trapped, are also indicated. We trapped this female on June 24. At least six or seven of her 12 nipples had been recently used.

The male dug but one new burrow during our stay, and cleaned out many established ones during the last week of June. This animal showed very little fear of birds: two gulls were once sitting within 5 feet of him, and a rock ptarmigan took its dust bath next to him at the entrance to his den, without alarming him in the slightest. The voracity of this animal was surprising: one morning he ate, and stored away, at least 3 pounds of caribou meat. We dug out two burrows in an effort to locate his cache, but could not find any meat. One burrow was 33 inches long, and slightly curved. The other was 53 inches long and had a side fork of 18 inches. Both burrows were about 15 inches at the deepest, which is at permafrost level.

Based on the activity pattern of the male squirrel and observations made of other ground squirrels, it appears that these mammals are most active in June during early morning hours, less active in the afternoon, and inactive between 18:25 and 4:00 s.t. At least, no observations were made during the latter period, although we were out and about regularly. This

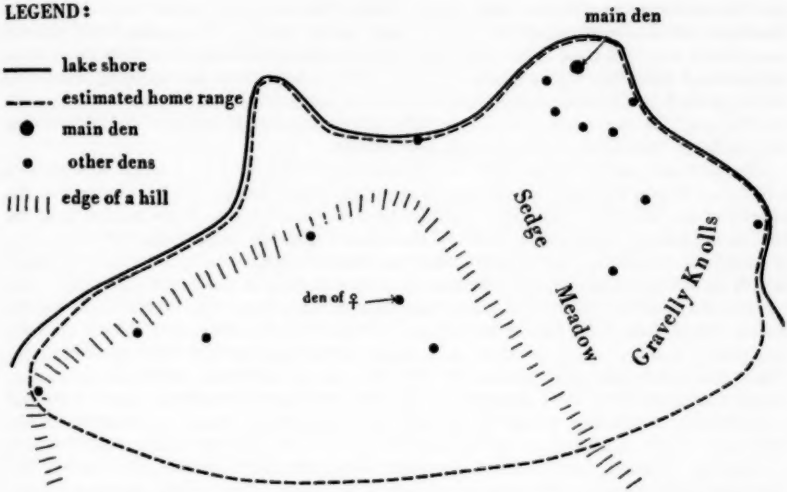

FIG. 1.—The estimated home range of a male Arctic ground squirrel. The dotted area encloses roughly 10 acres.

is interesting because of the continuous daylight and because these animals have only a restricted period of activity between hibernations. The longest period during which the animal was largely active was 8 hours, starting at 7:45. On most days, rest periods lasting from half an hour to 5 hours in duration were taken. The male ground squirrel spent each night, as well as rest periods during the day, in his main den. He was heard chattering several times when he emerged from his den early in the morning. Once he chattered at ducks passing over. He was once seen visiting the burrow of the female in his home range. Sunning was often indulged in, but for short periods only. Generally, this animal appeared to be most active on sunny, warm days. On June 17, when it was cold, overcast weather with high winds, he did not surface at all.—ANTOON DE VOS, *Ontario Agricultural College, Guelph, and* EDWARD M. RAY, *Michigan Dept. of Conservation, Roscommon.* *Received September 8, 1958.*

PEROMYSCUS NASUTUS IN NORTHEASTERN NEW MEXICO

On June 11, 1955, small mammal trapping in Quay County, 8.5 miles south of San Jon in northeastern New Mexico, resulted in the capture of one specimen each of *Perognathus merriami, Peromyscus maniculatus, Peromyscus boylei* and *Peromyscus nasutus.* The selected trapping site was on a northward facing escarpment representing the southern wall of an old river valley through which now flows San Jon Creek. This creek flows into the Canadian River toward the east, and the width of the valley is approximately 16 miles. No large canyons lead from the rim to the valley below, but numerous arroyos have dissected the escarpment.

At the trapping site the soil was quite red and rocky and, except for the presence of piñon pines, there was little difference between the vegetation of this area and that of the canyons of northern Texas. The juniper–piñon association characteristics of the Navahonian Biotic Province of Dice (The Biotic Provinces of North America, Univ. Mich. Press, 1943)

was the dominant association. Piñon pines occurred on the more gentle slopes leading to the river valley as well as on the steeper rocky areas. None of the piñon trees were of exceptional size, and most were under 10 feet in height. Scrub oak and *Schmaltzia* were encountered with the dominants in scattered clumps throughout the trapping area, and other plants that occurred in small quantities were mesquite, acacia, cholla, beargrass and prickly pear. The dominant grasses were dense only in places embodying favorable conditions and included *Bouteloua, Setaria, Triodia* and *Hilaria.*

The previous eastern range limit of *Peromyscus nasutus* in New Mexico was Bailey's (N. Amer. Fauna 53, 1931) record from Tucumcari, Quay County, and the presence of this species at the San Jon locality, only 10 miles from the New Mexico–Texas border, is of importance when the relationship between this species and the related species *Peromyscus comanche* is considered in terms of Pleistocene climatic shifts. The species *nasutus* ranges widely in the mountains of New Mexico where it is limited to the piñon–cedar and other montane associations. The closely related species *comanche*, apparently derived from *nasutus* (Blair, Contr. Lab. Vert. Biol., Univ. Mich., 24: 1–8, 1943), has a range limited to cedar associations in deep canyons along the escarpment of the high plains of the Texas Panhandle. These two populations are separated by over 80 miles of unsuitable ecological associations which effectively limit their distribution. At one time these populations must have had a continuous distribution across the plains which may have existed as recently as late Wisconsin (Blair, Evolution, 4: 253–275, 1950) and extended as far south as the Balcones Escarpment in south central Texas (Tamsitt, Texas Jour. Sci., 9: 355–363, 1957). The post-Wisconsin climatic shifts toward aridity in the high plains would account for the elimination of the populations from the plains and for the isolation of a segment of the population along the escarpment of the plains (Blair, *op. cit.*). It is likely that the post-Pluvial increase in aridity in the high plains limited the eastern range of *nasutus* in this region to the canyons of the Canadian River and its smaller tributaries.

The single male specimen of *Peromyscus nasutus* (Texas Nat. Hist. Coll. 5019) obtained from this locality does not differ significantly in skin and cranial measurements from specimens of this species from Lincoln County, New Mexico (Table 1). One cranial character, however, appears to be intermediate between this and the species *comanche*. The most conspicuous skeletal difference between the two species is in the shape of the interparietal (Blair, *op. cit.*, 1943). This bone is roughly elliptical in *nasutus* but is triangular in *comanche*. In the San Jon specimen the interparietal is somewhat triangular in shape. Thirty specimens of *nasutus* in the Texas Natural History Collection of The University of Texas were examined, but in only one of these did this bone appear to be slightly triangular.

TABLE 1.—*Average dimensions (in mm.) and range of 28 Peromyscus nasutus from Lincoln County, and measurements of the specimen from San Jon, Quay County, New Mexico*

CHARACTER CONSIDERED	LINCOLN COUNTY, NEW MEXICO	QUAY COUNTY, NEW MEXICO
Total length	210.2 (186–230)	195
Body length	102.5 (90–116)	96
Tail length	107.1 (85–118)	99
Ear length	22.0 (19.4–23.5)	21.7
Skull length	28.7 (27.3–29.6)	27.8
Parietal-bullar depth	10.0 (9.4–10.5)	10.4
Interparietal length	10.6 (8.9–11.4)	10.7
Interparietal width	3.6 (2.9–4.3)	3.7
Bullar length	5.0 (4.6–5.4)	5.1
Bullar width	3.3 (2.9–4.0)	3.8

Although the interparietal in *comanche* and *nasutus* appears to be less variable in shape than in the related species *truei*, additional specimens might have indicated if this peripheral population had an exceptional variation in this character.

The writer is gateful to W. Frank Blair of The University of Texas for suggesting the trapping locality and for reviewing the manuscript.—J. R. Tamsitt, *Dept. of Zoology, Univ. of Manitoba, Winnipeg. Received June 19, 1958.*

SURVIVAL OF HAMSTERS ON CALIFORNIA RANGELAND

To test the adaptability of the golden hamster, *Cricetus auratus*, to foothill range conditions in central California, 37 individuals were released at various times between June, 1948 and November, 1950 in a 50 × 100 ft. rodent-proof pen at the San Joaquin Experimental Range, O'Neals, California. Only ten of these animals survived as long as one week. Six lived more than two weeks. One of the latter, an adult male, survived for more than 7 weeks but died in a trap from exposure to the morning sun.

At first, all animals lost weight, but those that survived more than two weeks started gaining it back. If hamsters can do this well in the unfavorable conditions of the enclosure, with no supplementary food, it seems probable that they could become established where food and cover were more favorable.

To compare the survival of hamsters with that of native rodents in the pen, and to make sure that the pen was escape-proof, 16 native rodents—five kangaroo rats (*Dipodomys heermanni*), three pocket mice (*Perognathus inornatus*), and eight white-footed mice (*Peromyscus boylei*)—were also released in the pen at various times. They were originally captured just outside the pen. Live traps were regularly set both inside and outside the pen. The pen was apparently rodent-proof as none of the native rodents were ever recaptured in their former home range outside the pen.

Four of the five native kangaroo rats released in the pen had a fairly good survival rate. One lived at least 82 weeks, and was retrapped 16 times. One lived 25 weeks and died in a trap. The other two lived 23 and 18 weeks, respectively.

Only one white-footed mouse was known to have lived more than one day; it was retrapped four times during six weeks. Hamsters, therefore, survived longer than white-footed mice, but not as long as kangaroo rats.

All rodents released in the pen were vulnerable to hawks and owls, especially when traveling along the edges of the pen in attempts to escape. Once the rodents had discovered a burrow system, none of them were ever observed wandering about the pen in the daytime. It is not known to what extent hamsters excavated their own systems, because they customarily occupied systems made earlier by pocket gophers (*Thomomys bottae*) and kangaroo rats. (This is also typical of native rodents, which usually occupy existing systems rather than dig entirely new burrows.)

About ⅔ of the pen is covered with annual grasses and herbs; the remainder has a canopy of woody vegetation: one 30-ft. blue oak (*Quercus Douglasii*), a 15-ft. Digger pine (*Pinus sabiniana*), two coffee berries (*Rhamus Californica*), and 20 wedgeleaf ceanothus (*Ceanothus cuneatus*). The golden hamsters used in this experiment were furnished by Karl F. Meyer and Karl T. Brunner, of the George Williams Hooper Foundation for Medical Research, and by the West Side Hamstery, Tracy, California.

This study indicates that the domesticated strain of golden hamsters sold by pet stores or used in scientific laboratories could become a serious threat to California rangelands, as a feral population, if the animals were released near favorable food and cover and not controlled before they started to breed.—Walter E. Howard, *Field Station Administration, Univ. of California, Davis. Received September 17, 1958.*

OBSERVATIONS ON A CAPTIVE SHORT-TAILED WEASEL

On October 3, 1957 near Ithaca, New York, a male *Mustela erminea cicognani* was captured in a live trap baited with peanut butter and rolled oats set at a *Microtus* runway. Showing every indication of normal health and activity it was kept for three weeks. Live *Peromyscus* were fed to the weasel periodically; they were readily killed and eaten, and were supplemented by canned commercial dog food, the main constituent of which was horse meat.

At the end of the three weeks a live *Peromyscus leucopus* was introduced as food. The weasel quickly grasped it firmly at the base of the skull. The weasel then rolled over on its right side and lay still. The mouse struggled until it released itself, whereupon it ran to the far end of the cage. The weasel suddenly arose and with the usual burst of speed again caught the mouse at the base of the skull. Again it fell over on its side after having obtained a good hold on the mouse. The mouse escaped once again and the performance was repeated a third time —but this time the weasel could only grasp the tail of the mouse near the proximal end. The hold was so feeble, however, that with a little encouragement with a probe the mouse pulled its tail free and left the weasel again lying on its right side. After about 10 minutes the weasel stopped breathing and the heart beat grew fainter until death ensued. The mouse was unharmed and lost its fear of the weasel completely after the third encounter.

When the weasel's skull was cleaned the teeth were observed to be in an extremely worn condition. All cusps were worn down completely and the canines were worn to nearly the same length as the outer incisors on both jaws. The upper right canine was broken off flush with the maxillary bone. These indications of old age gave the only clue to the cause of death. The internal organs were in healthy condition and free from any observable parasites. The weasel, in summer pelage, measured: 268.7—74.0—35.4 mm.; 67.4 grams. The testes measured 6 × 4 mm. The specimen is No. 9722 in the Cornell University collection.—D. R. SEIDEL, *Conservation Dept., Cornell University, Ithaca, N. Y. Received August 1, 1958.*

THE WOLVERINE AND FISHER IN THE YOSEMITE REGION

The wolverine (*Gulo luscus luteus*) is one of the rarer mammals of the Sierra Nevada Mountains and, while it has been reported previously from the region of Yosemite National Park, Cahalane (Jour. Mamm., 29: 249, 1948) states that "the last unquestionable record for Yosemite was made in 1932." Since that time several observations have been recorded.

In August, 1951 an animal accurately fitting the description of a wolverine was observed at Upper McCabe Lake (10,480 ft.). In July, 1952 a visitor described seeing a wolverine, illuminated by the car's headlights, on the Tioga Road (Hwy. 120) near the May Lake trail junction (8,900 ft.). In August, 1952 George Templeton, of the Sierra Club, observed a wolverine take shelter under a large, split boulder near Mono Pass (10,560 ft.). The boulder was approximately 8 feet high with a cleft down the middle large enough for a man to enter. Alpine Fell-field and Subalpine Forest (Munz and Keck, El Aliso, 2: 87–105, 1949) vegetation, interspersed with boulders, surrounded the site. Several clumps of whitebark pine (*Pinus albicaulis*) were growing nearby. A photograph of the habitat was made and is on file in the Yosemite Museum.

On June 10, 1953 a visitor reported seeing two wolverines approximately a mile apart off the Tioga Road, 6 miles east of Crane Flat (7,000 ft.). Both were observed near a stream at about 4:30 PM on a sunny day. Another was observed at a distance of 50 to 75 feet near Mono Pass on August 25, 1953 by Robert Jacobson.

There are also several older records on file in the Yosemite Museum. At about 3:00 PM in October, 1929 a wolverine was observed "near the little lake going over [the] pass of [the] Lyell Fork towards [the Park] boundry" by District Ranger John Bingamon. Other notes indicate that wolverines or their tracks have been observed from Saddlebag Lake (10,051 ft., July 1929), Elwell Meadow, Lundy Lake (7,766 ft., summer 1939), near Tilden Lake (8,900 ft.), near Wegner Lake (9,300 ft., 1937), and at the foot of the Lyell Glacier (13,000 ft., August 28, 1941).

Borell (Yosemite Nature Notes, 12: 62, 1933) lists the wolverine as occurring also at Breeze Lake and Huckleberry Lake. Other recent wolverine findings in the Sierra Nevada have been recorded by Ruth (Jour. Mamm., 35: 594, 1954) and by Jones (*ibid.*, 36: 569, 1955).

On July 2, 1954 a fisher (*Martes pennanti*) and two young were observed at the Pictograph Site along Bridalveil Creek at 6:15 PM by Robert N. McIntyre. His notes state: "At a distance of 60 feet [I] observed two animals which I believed to be pine marten across the creek, but suddenly an animal over twice their size appeared and upon spotting me made a rush in my direction as close as the creek some 20 feet away and snapped its teeth at me in a belligerent manner. After looking me over carefully it retreated with a burst of speed in the direction taken by the two smaller animals."

Ware (Yosemite Nature Notes, 22: 80, 1943) reported sighting a fisher at mid-day near Bridalveil Creek Campground. Notes on file in the Yosemite Museum indicate that on March 19, 1927 tracks were observed near Tenaya Lake (8,141 ft.) and that the 1944 ski patrol observed a single fisher's track at the junction of the Ostrander trail on the Glacier Point Road. In October, 1942 L. C. Danner observed a fisher carrying a fish it had captured at Tenaya Lake.—JOHN D. CUNNINGHAM, *University Elementary School, Univ. of California, Los Angeles 24. Received August 6, 1958.*

BATHING BY SPOTTED HYENAS IN UGANDA

Although the spotted hyena, *Crocuta crocuta*, is distributed throughout Africa south of the Sahara (excepting the forests of west Africa and the Congo Basin) and within its range occupies an astonishing diversity of habitat from desert scrub to mountain forest, there is probably no one region in which it is more plentiful than the terrain that surrounds Lake Edward in Queen Elizabeth Park, Uganda. On one occasion in October, 1957, C. Jackson Selsor and I counted 18 specimens in view simultaneously, and park warden Frank Poppleton assured us that he had been confronted with as many or more hyenas on a number of occasions. Although generally considered to be a nocturnal species, the spotted hyena is represented in the Lake Edward district by examples that are active and visible to park visitors throughout the day. This condition renders observation of the species far easier than in unprotected areas where hyenas are less active diurnally and have not attained such a degree of superabundance.

One aspect of spotted hyena behavior that may readily be observed in Queen Elizabeth Park, yet which has not to my knowledge been previously recorded elsewhere, is the use of water for bathing purposes. On two successive mornings, just at dawn, we observed hyenas, both singly and in small groups, moving down the scrub and euphorbia-covered slopes at the northeastern end of Lake Edward. Upon arriving at the lake shore, the hyenas paused to drink briefly, then waded into the lake, some individuals proceeding as far as 10 or 15 feet from the shoreline and until the water level reached their abdominal regions. One group of bathing hyenas consisted of ten individuals including three or four half-grown pups that cavorted playfully, chasing one another through the shallow water. On several occasions, adult hyenas lowered themselves into the water until only their heads protruded above the surface. In no instance did we witness any activity that could be interpreted as swimming rather than wading. The bathing process was often a prolonged affair; one group of hyenas remained in the water for more than half an hour.

During the more than two decades in which I was connected with the San Diego Zoological Gardens and throughout which period spotted hyenas were exhibited by that institution, I observed in them no interest in water for other than drinking purposes. Nor have I observed non-captive hyenas bathing in lakes, rivers or ponds elsewhere in central, eastern or southern Africa, even in areas where both spotted hyenas and water were abundant. Perhaps the free use which Queen Elizabeth Park hyenas make of water may be correlated with the complete absence of crocodiles from Lake Edward.—KEN SCOTT, JR., *1674 Cable St., San Diego 7, California. Received June 4, 1958.*

REPRODUCTIVE AND VOCAL BEHAVIOR IN CAPTIVE PUMAS

With regard to the breeding activity of the puma, *Felis concolor*, Young (*in* Young and Goldman: THE PUMA, MYSTERIOUS AMERICAN CAT, Amer. Wildlife Inst., 1946) stated that "Aside from the regular menstrual [*sic*] periods the female comes into heat almost immediately after the young are born; the period of heat approximates 9 days. . . . The animals are at least 2, and probably 3, years old when they begin breeding." The following notes add to the few gestation estimates in the literature and partly corroborate the above statements, for which no specific records were cited.

The puma Tina was born at the Chicago Zoological Park on June 27, 1954. She first came into heat in November, 1956, at the age of 2 years and 5 months. As in all her ensuing estrus periods, this time was marked by persistent yowling or caterwauling much like that of the domestic cat, but amplified and harsher. The cries were frequently given from a crouching position, especially during the middle of her periods. Nonvocal estrus behavior included rubbing the perineal area against the ground, brushing frequently against the sides of the cage, more amiable responses to human attentions such as scratching, and reduced feeding. The vulva was noticeably moist at these times, but no vaginal discharge was seen.

As measured by the vocalization, of nine periods to date the longest was 11, the shortest and the mode were 8 days. From February 13 to June 17, 1957 there were six rather regular periods. An average of 14.4 days elapsed from the end of one to the beginning of the next, and an average of 22.8 from the beginning of one to the start of the next. Sixty-three days passed from the end of estral activity in June to August 19, when she began a ten-day period. During the last eight days of this period a male puma from Montana was introduced into the cage. As a result, two cubs were born November 19. One was probably dead at birth, the other survived for two days. Gestation was not less than 82 nor more than 90 days. Seventeen days later Tina was in heat for eight days and was mated with the same male. The subsequent gestation period of 88 to 92 days resulted in the successful birth of three cubs on March 10, 1958. In the following 2½ months, while the cubs were with her, no evidence of estrus was noticed. The lesser figures in the gestation estimates were counted from one day after initial mating, which presumably induces ovulation in the puma as in other cats. The extremes recorded for the puma seem to be the first period given above and the instance of 98 days reported by Allen (Jour. Mamm., 31: 279–80, 1950).

Before introduction into Tina's cage, the male replied to her cries with less loud yowls of his own. Her reception of him was far from cordial. A great deal of sparring and snarling on her part preceded mating and he responded in the same fashion, but not so vigorously. Most of the time they lay about in armed truce. At other times Tina would roll on her back, tread a wooden block, and in general become "kittenish."

Copulation was brief, less than a minute in the instances observed. The male was seen to grasp Tina's neck fur on some of these occasions. With his ordinary mate this male has been seen attempting copulation in a ventral–ventral position and engaging in post-copulatory licking of his mate's head and neck fur.

With respect to the puma's reputation for silence, it may be that pumas in the wild, as in captivity, usually do not cry except during estrus. This would account for the infrequent records when considered with the biannual breeding cycle of most females (cf. Young and Goldman, *op. cit.*; McLean, Calif. Fish and Game, 40: 147–66, 1954). In addition to the yowling estral calls, the puma Tina has made a variety of sounds similar to those of the domestic cat. Most unlike the latter were the loud squealing whistles of her young which were heard for three months after birth. Apparently this sound is usually an attention-seeking action but occasionally it is given in play or with no obvious connection. In two other young pumas observed for a longer period, the whistling changed at the age of 3½ months in the direction of the generally shorter and lower-pitched mewing whistle made by at least some captive adults (the latter reported by Robert Bean *in* Cahalane, MAMMALS OF NORTH AMERICA, Macmillan, 1947).

I wish to thank Glennis Bushor and W. M. Williamson, whose observations have been freely incorporated above.—GEORGE B. RABB, *Chicago Zoological Park, Brookfield, Illinois. Received July 11, 1958.*

SHARKS AS ENEMIES OF SEA OTTERS

During the last half of 1957 and early 1958 approximately 17 sea otters (*Enhydra lutris nereis*) were found dead along the coast of Monterey County, California, according to Captain Howard V. Shebley of the California Department of Fish and Game. Nine of these washed ashore between January 1 and March 20, 1958. Some of these casualties were attributed to spear wounds inflicted by skin divers although this was not definitely proved. One sea otter found on March 2 at Carmel Beach was reported to have been shot in the head.

Three sea otters (2 males, 1 female) that had been found dead at Pebble Beach on February 3, 4 and 6, respectively, and subsequently frozen, were brought to the California Academy of Sciences on February 21 to be preserved as specimens. All appeared to be subadults. The total length of the female was 1,072 mm. The males measured 1,103 and 1,090 mm. in total length. Although these animals were not in fresh condition when found, their skins were saved and careful autopsies were performed to determine, if possible, the cause or causes of death.

A series of gashes, arranged in the form of a semicircle, was present on the back of the female just behind the shoulders. In one of these wounds a portion of a shark tooth was found (Plate I). The larger of the two males had wounds on each side of the thoracic area, on the right side of the neck and on the back. The smaller male had a wound behind the left shoulder that extended into the thoracic cavity.

The nature of the wounds on the female plus the presence of the broken tooth made it appear likely that the death of this animal had resulted from an attack by a shark. The somewhat similar wounds on the larger male may also have been inflicted by a shark. The wound that likely was the cause of death of the third sea otter could have been produced by a spear.

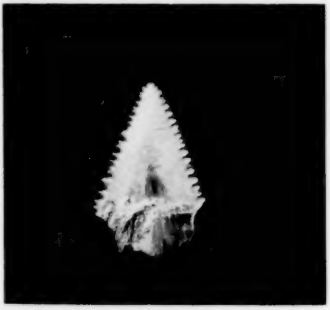

PLATE I

Apical fragment of tooth of a man-eater shark (*Carcharodon carcharias*) embedded in back of a subadult female sea otter (*Enhydra lutris nereis*) found dead at Pebble Beach, Monterey County, California, on February 6, 1958. × 1.23. Photograph by W. I. Follett.

The apical fragment of the shark tooth found embedded in the female was given to W. I. Follett, Curator of Fishes at the California Academy of Sciences, for determination. It was found to be an upper tooth (possibly the second) of a man-eater shark, *Carcharodon carcharias* (Linnaeus). On comparison with the teeth of other sharks of this species whose dimensions were know it was estimated to have come from a small individual approximately 9 feet in length. The man-eater or great white shark is not uncommon in California coastal waters. Within the past few years several swimmers have been attacked by man-eaters in the vicinity of Monterey.

So far as known, this represents the first record of predation on sea otters by man-eater sharks. However, in view of the increase in the sea otter population along the Californa coast in recent years, such incidents may not be uncommon. Perhaps the high mortality in the latter part of 1957 and early 1958 was largely the result of attack by sharks.—ROBERT T. ORR, *California Academy of Sciences, San Francisco and Univ. of San Francisco, California. Received August 11, 1958.*

A LABORATORY CAGE FOR SMALL MAMMALS

In an experiment designed to study the qualitative and quantitative aspects of forest tree seed consumption by small mammals, conventional cages for the care and handling of mice were found to be inadequate. Preliminary efforts to use one-compartment single-cover cages for the confinement of white-footed mice (*Peromyscus leucopus*) were very unsatisfactory.

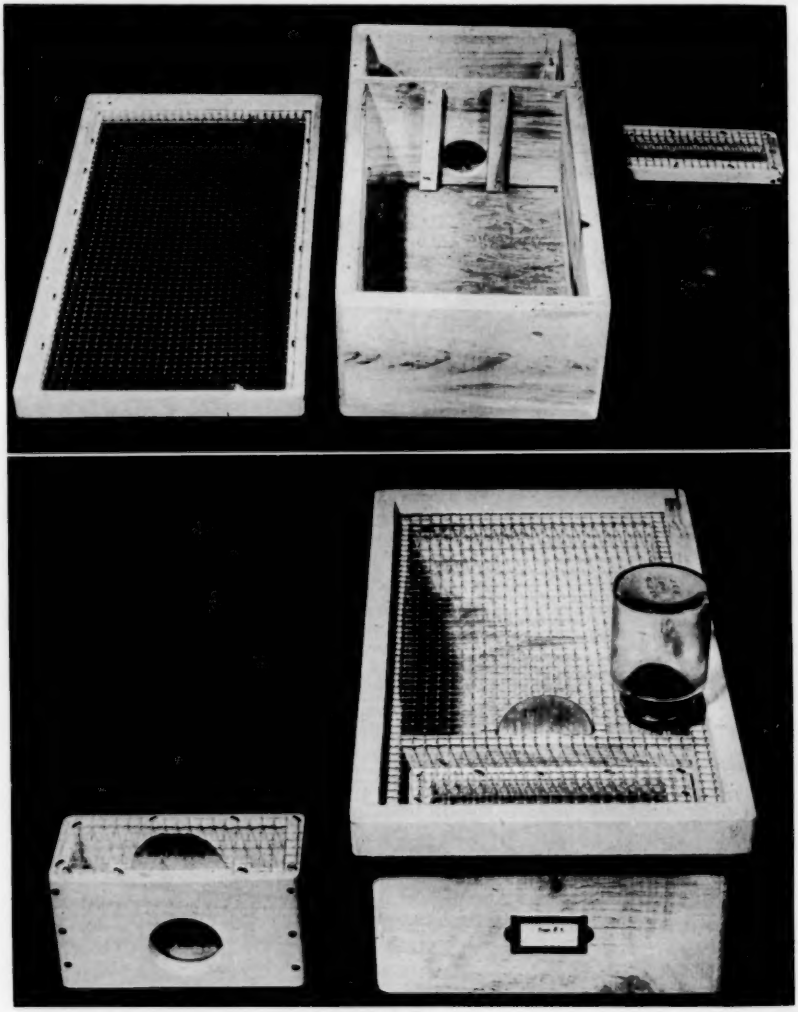

PLATE I

ABOVE: Photograph of main cage showing covers and sliding doors removed.
BELOW: Left—weighing cage; right—main cage assembled for use. Photos by Robert L. Coffin.

Cage sanitation, daily feeding schedules, and periodic determination of animal weights necessitated removal of animals from their cages each day. This frequent handling caused agitation to the mice, resulted in several escapes, and made laboratory maintenance of animals laborious and impracticable. Consequently, experimental work was delayed until a more suitable cage could be obtained.

Three rather simple but important features were believed to be essential in the type of cage desired if it were to meet the requirements of the experiment. First, it should have two compartments, one to provide the living quarters of the animal confined, and the other, smaller in size, to serve as a temporary confinement area when the larger compartment is being cleaned and food supplies replenished. Second, each compartment must have its individual cover in order that free access to either compartment by the laboratory technician be possible without permitting an opportunity for escape by the caged mammal. The third feature should be one which would make possible the easy removal of animals from the cage for any desired purpose without necessitating physical contact with the animals.

Since no cage could be found which had these essential features, one was designed which ultimately proved to be highly satisfactory for this food consumption study and which would appear suitable, with minor modifications, for the confinement and handling of most small mammals in the laboratory.

This cage (Plate I) was constructed of softwood lumber, 1 in. thick by 6 in. wide. The main body of the cage is a box-like structure approximately 10 in. wide by 18 in. long. The bottom of the cage consists of ¼-in. plywood. The cage is divided into two compartments by a single partition of ½-in. lumber located 3 in. from one end of the box. A passageway between these compartments is provided by a circular hole 2 in. in diameter centered in the partition with its lower edge ½ in. from the bottom of the cage. A small wooden guide fastened vertically on each side of the passageway is rabbeted to hold a piece of sheet metal serving as a sliding door which can be easily removed.

The cage has two covers. One fits over the entire structure and consists of a frame constructed of small strips of wood ¾ by 1⅛ in. This frame is rabbeted to overhang the sides of the cage by ⅝ of an inch. Hardware cloth of ⅜-in. mesh is fastened to the underside of the cover with staples. A slit cut in the wire permits the insertion and removal of the vertically sliding door separating the two compartments. The cover for the smaller compartment also consists of a wood frame on which is stapled a small piece of mesh wire. This cover fits inside its compartment and is supported by a small piece of wood nailed in each corner. The small cover thus does not interfere with the large cover.

The caged animal can be easily transferred from the larger to the smaller compartment with a little urging. The sliding door of the partition, which is normally kept in place, is first removed and the animal is then encouraged to enter the smaller compartment. Upon replacing the door, the animal is securely confined and the cover of the main cage can be removed.

In order to facilitate the removal of the caged animal for weighing or for other purposes, an additional cage was constructed of such size that it could be inserted into the smaller compartment of the main cage. This small "weighing cage" (Plate I) is made of ½-in. lumber 3¾ in. wide. The bottom is made of ¼-in. plywood, and the top is enclosed with mesh wire attached with staples. Its outside dimensions allow it to fit readily within the smaller compartment with sufficient space between its ends and the sides of the main cage to permit easy removal. One side of this cage has a circular hole 2 in. in diameter cut to coincide with the hole in the partition of the main cage. Small pieces of wood rabbeted to hold a small removable sliding door, similar to the one previously described for the opening in the compartment partition, are nailed on either side of this entrance hole on the inside of the weighing cage. This allows the smaller cage to fit snugly against the partition. When the weighing cage is in place, the animal, in passing from the larger to the smaller compartment, becomes entrapped in a removable cage. By merely inserting the smaller of the two metal doors, the animal can be taken from the main cage to be weighed, transported, and otherwise handled as desired without human contact.

One criticism which has been made of this cage is that, being constructed of wood, it will therefore be subject to gnawing by the animals confined. Experience to date, based on keeping white-footed mice in each of five different cages for a period of six months, suggests that such criticism is not justified. If the wire of the main cover of the cage fits closely to the top of the cage and its partition, little gnawing should be experienced except possibly on the small pieces of wood which hold the compartment door in place. This did occur in one instance, but was quickly terminated by attaching a small piece of mesh wire over that part of the partition supporting the door. A 2-in. hole cut in the wire opposite the opening through the partition allowed for movement of the animal through the passageway. No further gnawing occurred.

By modifying slightly the construction of the cage, particularly the door in the partition, a metal liner could be inserted into the living quarters of the cage. For that matter, the entire cage could be constructed of metal, but with more difficulty and at somewhat higher cost. A definite advantage of the wooden cage is the ease with which objects such as removable feeding trays can be firmly attached to its sides. It also provides for better insulation against thermal changes than do metal cages. The wood absorbs moisture and thus contributes to a drier environment in the living quarters of the animal. With only approximately 3 board feet of lumber and 1 square foot of plywood required, it is economical as well as easy to construct. A carpenter can make several of these cages in one day.—Herschel G. Abbott and Dana P. Snyder, *Dept. of Forestry and Wildlife Management and Dept. of Zoology, Univ. of Massachusetts, Amherst.* *Received August 11, 1958.*

[Contribution No. 1167 of the Massachusetts Agricultural Experiment Station, Amherst.]

PREPARING MUMMIFIED SPECIMENS FOR CLEANING BY DERMESTID BEETLES

When old, hard, dry specimens are presented to dermestid beetles, they either do not clean them at all or do an unsatisfactory job of it. We have developed a simple method of preparation of this kind of material for the dermestid room that gives the same quality of finished skulls and skeletons that we get with freshly dried specimens. The process is as follows:

1. Place specimens in concentrated ammonia water for 3 to 12 hours, depending on size.
2. Soak in several changes of water, 3 or 4 at least, for a total of 2 or 3 hours.
3. Dry, but not hard.
4. Place in dermestid room.

We have had excellent results with all small vertebrates. In the past two years, we ran through the dermestid room hundreds of small skulls and skeletons that had been packed in borax for 15 to 20 years. We presoaked these in water 6 to 8 hours, changing the water several times, then put them through the process as outlined above. All specimens were promptly and thoroughly cleaned.—Leslie D. Case, Sr., *Museum of Zoology, Univ. of Michigan, Ann Arbor.* *Received August 29, 1958.*

REVIEWS

Hall, E. Raymond and Keith R. Kelson. THE MAMMALS OF NORTH AMERICA. The Ronald Press Co., New York. 2 vols., xxx + 1162 pp., 553 figs., 500 maps, 186 sketches. March 31, 1959. Price, $35.00.

This monumental work on the living mammals of our continent, long awaited and much publicized, will be heartily welcomed by mammalogists everywhere. For the first time, in one place, is such thorough treatment accorded all the recognized species of Recent mammals of the entire continent, including Greenland, all of Panamá, the Greater Antilles, and the Lesser Antilles through Grenada.

The authors are well known to readers of this Journal; both have served as officers of our Society and have been in frequent attendance at its meetings. Both have contributed notably to the literature on systematics and distribution of North American mammals. Dr. Hall is Director of the Museum of Natural History and Chairman of the Department of Zoology at the University of Kansas, as well as Director of the State Biological Survey of Kansas. Dr. Kelson is a staff member of the National Science Foundation, currently engaged in developing programs of science education, as well as a member of the Division of Biology and Agriculture of the National Research Council.

The books are large (8× 10¾ in.) and weigh 8 lb. 14 oz. The paper is of good quality, the binding of sturdy buckram, the type clear and legible, and the illustrations well reproduced. The text is set in a two-column format except for some of the longer keys. In the Preface the authors explain the over-all problem and their methods of attacking it. Following the Contents is a brief, general section (by Hall) on Zoogeography. The body of the work treats the various taxonomic categories of mammals, in supposed phylogenetic sequence, and includes 3,679 species and subspecies. The Heteromyidae conclude Vol. I and the Castoridae lead off Vol. II. There is a brief general description of each order and a detailed listing of traits of all families. Common names are provided for all species. Diagnoses are given for all taxa above subspecies, with appropriate keys. Measurements are listed and there are concise notes on habitat, foods, breeding, habits, etc. Subspecies are listed alphabetically and for each are cited original description, first usage of current name-combination, primary synonyms, and marginal records of occurrence; there are no aids to identification of subspecies except on geographic grounds. Following the systematic treatment is a general and useful section, albeit a bit cumbersome to take afield, on Collecting and Preserving Specimens. The Literature Cited occupies 30 pages and lists over 1,300 titles. The work aims to include all pertinent taxonomic and distributional information up to October 31, 1957. Five pages of Addenda include two new subspecific names and several marginal records that had been overlooked, as well as numerous recent additions bringing the record up to August 30, 1958. Separate Indexes to vernacular and technical names appear to be complete and well organized. The end papers contain attractive and helpful maps of the continent, showing political divisions and life zones.

In a work of this scope it is not surprising that some typographical errors have persisted, e.g., *Ziphus* for *Ziphius* (p. xix), *Crystophora* for *Cystophora* (p. xxii), and *Noctilieo* for *Noctileo* (*sic*, p. 51 of Index). There are other matters of style that seem not to have been standardized. On p. 1040 we read *cornmeal*, but on p. 1042 *corn meal*; on p. xxv, *salt water* appears on line 13, *saltwater* on line 19; on p. 596 is a reference to "2 to 5 young in a litter," and on p. 1042 are mentioned "eight to ten small mammals." In the Addenda (p. 1080), the reference to "Lowe (*loc. cit.*)" pertaining to *Sylvilagus aquaticus* is not easily traced. Throughout the work, in the legends to the 538 figures of skulls, the letter X is used instead of the times sign (×) for scale of magnification.

Abbreviations of teeth and use of dental formulae require explanation; not all readers are familiar with the senior author's usage (as in AMERICAN WEASELS, 1951) of capital and lower case letters to designate teeth of the upper and lower jaws, respectively. Particularly perplex-

ing to neophytes is the mention (p. 1003) of the p3 and P4 in deer, while the formula immediately beyond indicates only three premolars above and below. Similarly, the reference (p. 609) to both "1st and 2nd upper molars" and to "m1 and m2" in inconsistent.

This work, regarded as something of a centennial publication, is dedicated to the memory of Carl von Linné and of Spencer Fullerton Baird, whose classic works appeared in 1758 and in 1858. The 10th edition of Linnaeus' SYSTEMA NATURAE contained 184 species of mammals throughout the known world; Baird's MAMMALS OF NORTH AMERICA [Reports of Exploration and Surveys . . . for a Railroad from the Mississippi River to the Pacific Ocean] listed 256 species of North American mammals exclusive of the bats, pinnipeds and cetaceans; Miller's 1924 LIST OF NORTH AMERICAN RECENT MAMMALS recognized 1,399 species. Hall and Kelson now treat 1,003 species, although admitting that this number "is still too large" and predicting that further study will reduce it considerably, as by the possible lumping of the 77 species of grizzly and big brown bears. This project was begun in 1945 and carried through with financial assistance from the Office of Naval Research, the National Science Foundation and the Atomic Energy Commission. In the Preface, mention is made that "Remington Kellogg greatly assisted us." Gratitude is expressed to the University of California Press and to seven individuals for assistance. Finally, "in decreasing order of total time devoted to the preparation of the present volume," there are listed 10 artists, 8 typists and 30 others who participated. Now, as all biologists know, the present inventory of North American species has been compiled through the combined efforts of many hundreds, or even thousands, of workers. Singling out the few listed, and neglecting to mention any of the private or public collections or institutions upon which much reliance was placed, smacks of either arrogance or ingratitude.

The range maps may well prove to be the most useful feature of these volumes. Most common species (or subspecies) are mapped, except for marine forms. Listed in the text are Marginal Records, arranged in clockwise fashion, describing the periphery of the range; these correspond with dots on the accompanying maps. This system points up the cogent data without cluttering up the map unnecessarily with less relevant information. But herein lies one pitfall, for the shaded areas connecting the dots are in many cases the opinions of the authors, though not perhaps of other workers. The delineation of the range of *Hylonycteris underwoodi* (Map 85), for instance, seems fanciful and arbitrary. There is no apparent justification for including Louisiana and Mississippi in the range of *Sorex longirostris* (Map 14), and in the case of *Condylura* (Map 42) records for North and South Carolina (Jour. Mamm., 4: 183; 36: 288) were overlooked. Map 211 leaves the Laborador race of *Marmota monax* peculiarly disconnected from the other eight subspecies. Judging by Maps 261–266, the West is fairly teeming with *Thomomys umbrinus* (214 subspecies are recognized)! It is unfortunate that dates represented by the maps are not clearly indicated. Thus the ranges of the grizzly (Map 452), moose (Map 493) and bison (Map 496) are those in the historic past, while Maps 1, 178 and 443 depict the opossum, armadillo and coyote approximately as they are today. No map is provided for the nutria (p. 799), but under Some State Records there are listed 10 states where it occurs; actually the species is now established in the wild in 16 states and reported as present in at least 10 others.

The keys, designed to assist in identification of all difficult forms down to species, and accompanied in most cases by figures of skulls, combine measurements, dental traits, color characters and other features, with at times a heavy leaning on geographic grounds. Most of them seem workable. Some appear newly composed, while others are lifted, verbatim or with slight modifications (though not always credited), from earlier literature. For example, the key to genera of Talpidae (p. 66) follows that of Jackson (N. Amer. Fauna 38), that to species of *Spermophilus* (p. 336) is after A. H. Howell (N. Amer. Fauna 56), and that to species of *Phenacomys* (p. 718) is taken from A. B. Howell (N. Amer. Fauna 48).

One quarrel which mammalogists will have with Hall and Kelson concerns their treatment of scientific names. This work is not a critical review or a revision of any groups—such findings have previously been published elsewhere—but rather a compendium of

information for general reference, an extensive annotation of Miller and Kellogg's 1955 LIST OF NORTH AMERICAN RECENT MAMMALS, so to speak. This latter list, since its first edition in 1912, has been a standard of reference. In the present work, names of genera only which differ in usage are as follows:

Hall & Kelson	*Miller & Kellogg*	*Hall & Kelson*	*Miller & Kellogg*
Notiosorex	Megasorex	Hydrochaeris	Hydrochoerus
Rhynchonycteris	Rhynchiscus	Agouti	Cuniculus
Platyrrhinus	Vampyrops	Feresa	*not included*
Phyllonycteris	Reithronycteris	Speothos	Icticyon
Saguinus	Marikina	Ursus	Euarctos
Ammospermophilus, Spermophilus	Citellus	Bassariscus	Jentinkia
		Eira	Tayra
Oryzomys	Oecomys	Galictis	Grison
Neotoma	Teanopus	Arctophoca	Arctocephalus
Microtus	Orthriomys, Herpetomys, Pedomys, Pitymys	Tapirus	Tapirella
		Tayassu	Pecari
		Dama	Odocoileus

Some of these changes appear desirable, others are highly controversial. Some have been sanctioned by the International Commission, e.g., *Bassariscus* and *Speothos* (the latter particularly for fossil forms), but many have not. Our point is that, even though further standardization may be needed, this is not the place for it. One means of ruling on the validity of names is set up in the International Commission and, although tediously delinquent in rendering its opinions, they are nevertheless based on the thinking of a duly designated group and not on the subjective judgment of two authors. In this regard, the treatment by Hall and Kelson will do little to further the stabilization of mammalian nomenclature.

Herpestes, Mus and *Rattus* are treated in the text, but not *Bos, Capra, Equus* and *Sus*. There would seem to be as good reason for including the established domestic forms as the two genera of ground sloths (pp. 235–236). Professional mammalogists will be disappointed that the synonomies provided are in most cases the bare minimum (the cetaceans are a notable exception); amateurs may find the work too technical and will miss colored illustrations; both will balk at the unreasonable price, and both—if they scrutinize the system of pagination—will rebel at the nightmare which it poses.

Here and there occur statements which, to this reviewer, seem rather inept. On p. 234 we read that modern man is "characterized by having achieved the greatest degree of development of the generic characters." Under *Ochotona princeps* (p. 247) is the statement that "Eight Nevadan females had an average of 3.1 (2–4) embryos. The mode was 3." One cannot ignore the opinions, to which the junior author apparently could not subscribe, expressed on pp. 233–234: "Some authors have accorded separate family rank to man . . . because of an assumed wide gap in intelligence between man and the next most intelligent anthropoid. . . . Nor am I convinced that the gap in intelligence between some microgeographic races of man and some races of apes is very wide. . . . The morphological features . . . give basis for including gibbons, apes, and men in one family." This will furnish fodder for barbershop biologists for some time to come!

Such an opus as this cannot well avoid the inclusion of errors, both of omission and commission. Despite the criticisms voiced above, THE MAMMALS OF NORTH AMERICA stands out as a major landmark in North American mammalogy. The authors deserve the acclaim of their colleagues for the tremendous amount of labor that went into this compilation. There is no serious student but will consult it again and again. It is a summation of systematic American mammalogy to date and will certainly prove to be an indispensable reference to all specialists in this field.—RICHARD H. MANVILLE.

Hoffmann, Max. DIE BISAMRATTE; IHRE LEBENSGEWOHNHEITEN, VERBREITUNG, BEKÄMPFUNG UND WIRTSCHAFTLICHE BEDEUTUNG. 267 pp., 128 figs., 1 color plate. Akademische Verlagsgesellschaft Geest und Portig K.-G., Verlag Dr. Paul Schöps, Leipzig. 1958.

The author's background of nearly 30 years employment with the North American muskrat in Germany gives him extraordinary qualifications for writing his book. However, the book itself reflects European rather than North American experience and investigations, and it is also true that much of the European literature from outside of Germany is handled indifferently, at best. Coverage of the large North American literature may be regarded as particularly disappointing for, although many North American titles are listed in the extensive (42 closely packed pages) bibliography, little or even no reference may be made to them in the text, with most emphasis being placed on a few more or less obsolete publications.

The book may be described as understandably strong in some respects and weak in others. It contains no over-all treatment of population dynamics nor of ecological nuances in relation to the muskrat, but I do not feel critical because of what the author does not include within the scope of his book. The sections on food habits, diseases and parasites, predatory enemies, social relationships and movements consist more of presentation of individual facts than pertinent generalizations—still, the value of details to the specialist should not be overlooked. Part "C," dealing with the spread and distribution of the muskrat in Eurasia, should be of singular importance for reference purposes. Much the same may be said for part "D," on German control measures. Furthermore, there is a lot of information on anatomy (pp. 5–24), precocious breeding of young animals in the calendar year of birth (pp. 49–50), etc., that would be difficult to find elsewhere.

It is as a reference work that the book should be most useful for mammalogists—and I should think notably so for mammalogists who are already sufficiently familiar with muskrats and associated species to read with discrimination.—PAUL L. ERRINGTON.

Beck, W. H. A GUIDE TO SASKATCHEWAN MAMMALS. Saskatchewan Natural History Society, Special Publ. No. 1. Saskatchewan Museum of Natural History, Regina. 52 pp., 62 figs., 8 pl. 1958. Price, 50 cents.

This publication represents the first systematic attempt to list the mammals of Saskatchewan and to define their distributions. It gives accounts of 105 forms of 77 species, of which five subspecies and one species (*Myotis evotis*) probably occur in the province but have not yet been recorded. The introductory sections include brief descriptions of the physical features and life zones of the province. Most of the text is devoted to accounts of the species and subspecies of mammals that occur in Saskatchewan. Each account includes notes on habitat and range; color descriptions; measurements; and a list of localities from which the species has been recorded. With a few exceptions the distribution of each species within the province is represented by a map showing all of the localities for which museum specimens or literature citations are available. The distribution maps are exceptionally clear and informative.

Several species which have become rare or extinct over much of their former range in North America are still present, and sometimes abundant, in Saskatchewan. Notable examples are the black-footed ferret, river otter, wolverine and woodland caribou. An ambitious program of northern development is providing roads into the interior of northern Saskatchewan, and access into this area will undoubtedly stimulate more extensive study; but even the southern half of the province is poorly known in terms of mammal populations and distributions. It is noteworthy that even the common species are represented by only a few museum specimens and, hence, the distributional limits of many of the mammals of Saskatchewan are not in fact known. Wolverine are common in northern Saskatchewan but only one museum specimen is known from the province. Only six marmots have been collected and even the ubiquitous deer mouse is represented by only 31 specimens.

Recent collections indicate that substantial revisions of known distributions will be produced by future study of the mammals of Saskatchewan. Mr. Beck's brief but well-constructed guide will provide a valuable and orderly point of departure for such studies.—RICHARD S. MILLER.

Montagna, William. COMPARATIVE ANATOMY. John Wiley & Sons, Inc., New York. Pp. ix + 397, illus. March, 1959. Price, $6.00.

A new textbook for the semester-length course in comparative anatomy has been written by Dr. William Montagna of Brown University. Several convictions guided the author in his writing, three of which are mentioned here: (1) embryology is emphasized, (2) no undue emphasis is given the human, and (3) "allusions to fossil forms, reference to learned works, and terminology have been kept to a manageable minimum."

The first three chapters (40 pages) introduce the phylum Chordata, describe the characteristic body plan and its development (both ontogenetic and phylogenetic), and present some paleontology and a brief systematic classification. The remainder of the book deals with the anatomy of the various body systems. Each system is introduced by a general discussion of structure and function. A brief statement of developmental anatomy follows. Then, the meat of each chapter, the comparative anatomy of each system is described for the various chordate groups. A summary and a short, up-to-date bibliography complete each chapter.

Most of the text is well illustrated with excellent photographs and photomicrographs, and with line drawings. About one-half of the line drawings consist of black lines on a white background, the other half of white lines on a black background. This alternation of figure-background is heralded by the pattern of the dust jacket of the book. Key words are printed in a slightly heavier and darker type than the rest of the text. The book contains an adequate index and glossary.

Although the caliber of the book and its price should encourage its adoption and use, there are certain minor criticisms: Several of the white line drawings on the black background are noticeably marred by numerous white blotches on the background. The lack of illustrative material in the chapter on muscles, especially those of the appendages, and in the chapter on endocrines is regrettable. And although the key words are printed in a different and heavier type than the text, there is not enough contrast to easily and definitely attract the eye.—KENNETH L. DUKE.

Montagna, William and Walter Kenworthy. A LABORATORY MANUAL OF COMPARATIVE ANATOMY. John Wiley & Sons, Inc., New York. Pp. vii + 103. March, 1959. Price, $2.50.

This manual gives adequate instructions for laboratory dissection, but it must be supplemented by a textbook since it contains no illustrations. In the interest of that great thief, brevity, instructions are given for only the shark, necturus and the cat. Two chapters except this rule. The one on the endoskeleton includes material for the shark, necturus, frog, turtle, alligator, birds and the cat. On the other hand, the chapter on the nervous system and sense organs has material only for the shark and the cat.

The manual is so bound, with a plastic ring-type binding, that when it is opened and placed on the laboratory bench it stays open, the pages remaining down flat. Although key words are reproduced in a different and heavier type than the text, the contrast is not sufficient to be really eye-catching.—KENNETH L. DUKE.

RECENT LITERATURE

(Prepared by the Committee on Bibliography)

[Reprints of this bibliographic section may be purchased from the Secretary-Treasurer. However, the Society cannot furnish reprints of the individual publications listed.]

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AKOPYAN, M. M. Some problems of the improvement of trap-ground census taking of susliks. Zool. Zhurnal, 38 (2): 273–279. January 26, 1959. (In Russian, with English summary.)

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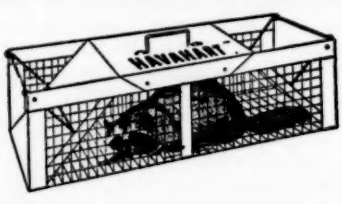
HAVAHART HUMANE ANIMAL TRAPS



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COMMENTS AND NEWS

COMMITTEE ON NOMENCLATURE

A newly constituted and expanded Committee on Nomenclature was appointed by President Orr at the Washington meeting. The committee met briefly on June 24, 1959, to discuss its program for the coming year. It was agreed that priority should be given to an attempt to stabilize the nomenclature of North American mammals. Inasmuch as the International Commission on Zoological Nomenclature has difficulty in handing down decisions, and then sometimes after long delays, your committee decided that it should take the lead in our particular area. The A.S.M. committee, therefore, will welcome inquiries on any questionable name, and will give an opinion on the proper name to use. Opinions, we hope, will be printed in the JOURNAL. If the committee cannot reach unanimous agreement, opinions of the various members, with their reasons, will be given, and the author can be governed accordingly.

Opinions of this committee will not be binding. The committee will work within the framework of the code of the I.C.Z.N., and will make recommendations to that body regarding names of North American mammals. Although not binding, it is the desire of your committee that its recommendations be followed so that stability can be attained.

The committee will confine its activities strictly to problems of nomenclature. Biological problems are not its concern.

STEPHEN D. DURRANT
E. RAYMOND HALL
CHARLES O. HANDLEY, JR.
PHILIP HERSHKOVITZ
DONALD F. HOFFMEISTER
BARBARA LAWRENCE
RANDOLPH L. PETERSON
HENRY W. SETZER
RICHARD G. VAN GELDER
WILLIAM H. BURT, *Chairman*

TO FOREIGN MEMBERS

The Society will hold its next annual meeting at Tacoma, Washington, June 20–22, 1960. The attendance of foreign members may be facilitated by a special letter of invitation from the Society. Requests for such letters should be addressed to the President, Dr. Robert T. Orr, California Academy of Sciences, Golden Gate Park, San Francisco 18, California, together with suggestions as to content and officials to whom the letters should be directed.

LALOR FOUNDATION GRANTS

The Lalor Foundation has announced its 1960 program of awards for support of research on the fundamental biochemical and physiological mechanisms concerned with fertility and reproduction in various forms of life. The awards range up to $8,000 per year, with preference given to college staff members under 45 years of age. In addition, smaller short-term post-doctorate awards are available for work at the Marine Biological Laboratory at Woods Hole, Massachusetts. The 1960 program follows closely the pattern of 1959, when 27 awards were granted. Information and application forms may be obtained from The Lalor Foundation, 4400 Lancaster Pike, Wilmington 5, Delaware. Deadline for receipt of applications with supporting data is 15 January 1960; appointees will be notified by 15 March.

DEATH REPORTED

Otis M. King, July 31, 1959

THIRTY-NINTH ANNUAL MEETING

THIRTY-NINTH ANNUAL MEETING OF THE AMERICAN SOCIETY OF MAMMALOGISTS

June 21–25, 1959

The thirty-ninth annual meeting of the American Society of Mammalogists was held at the United States National Museum, Washington, D. C., June 21–25, 1959.

Chairmen of the local committees were : Viola S. Schantz, General Chairman, Stewart M. Brandborg, Helen S. Gaylord, Charles O. Handley, Jr., David H. Johnson, Daniel L. Leedy, Richard H. Manville, John L. Paradiso, Clifford C. Presnall, Theodore H. Reed, Henry W. Setzer, Ernest P. Walker and Stanley P. Young.

PROGRAM

SUNDAY, JUNE 21

8:00 PM—Directors' Meeting at Harrington Hotel

MONDAY, JUNE 22

8:00–12:00 AM—Registration, Foyer, U. S. National Museum

9:00 AM—Morning Session, U. S. National Museum Auditorium

Welcome: Dr. Albert C. Smith, Director, Natural History Museum, U. S. National Museum.

Response: Dr. Robert T. Orr, President, American Society of Mammalogists.

1. Mammals of Glen Canyon. Stephen D. Durrant, University of Utah, Salt Lake City.
2. Distribution and abundance of prairie dogs in Colorado. R. R. Lechleitner, Colorado State University, Fort Collins.
3. Northward movement of *Baiomys taylori* in Texas. Gerald C. Raun and Don Hunsaker, II, Welder Wildlife Foundation and University of Texas, Austin.
4. An Illinoian glacial fauna from Oklahoma and its climatic significance. John J. Stephens, III, University of Michigan, Ann Arbor. (This paper was awarded an honorarium.)

1:00 PM—Afternoon Session

5. A live-trapping system for estimating population density. Don W. Hayne, Institute for Fisheries Research, Ann Arbor, Michigan.
6. Highlights of an 11-year live-trapping study at Flathead Lake, Montana. Philip L. Wright, Robert S. Hoffmann, Montana State University, Missoula, and Clinton H. Conaway, University of Missouri, Columbia.
7. Biotic communities, rodent reservoirs and arthropod vectors in relation to the transmission of tularemia, plague and anthrax in desert mammals. E. Dean Vest, Dale D. Parker, D. Elmer Johnson, Nyven J. Marchette and John B. Bushman, University of Utah, Ecological Research, Dugway.
8. Field studies on mammals at Oak Ridge National Laboratory. Paul B. Dunaway, Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
9. Mortality of cocoons of the larch sawfly in relation to the distance from small mammal tunnels. Charles H. Buckner, Forest Biology Laboratory, University of Manitoba, Winnipeg.
10. Habitat relationships of *Peromyscus floridanus*. James N. Layne, University of Florida, Gainesville.
11. Population ecology and taxonomic status of white-tailed deer in northeastern Alabama. William H. Adams, Jr., Wildlife Research Unit, Auburn, Alabama. (This paper was awarded an honorarium.)
12. Some aspects of the ecology and population dynamics of the pocket gopher, *Geomys bursarius*, in southern Texas. Bobby J. Wilks, University of Texas, Austin, and Welder Wildlife Refuge, Sinton

13. Observations on the life history of the antelope ground squirrel. Ormond G. Mitchell, California State Polytechnic College, Pomona.

7:30 PM—Smoker. Room 43, U. S. National Museum

Films: "Return of the Right Whale to New England Waters." William E. Schevill, Woods Hole Oceanographic Institute, Woods Hole, Massachusetts.

"Rabies in the Wild." Stephen H. Richards, Dept. of Veterinary Science, Game and Fish Dept., North Dakota Agriculture College, Fargo.

"Pacific Walrus." John L. Buckley, U. S. Fish and Wildlife Service, Washington, D. C.

Preview of the new World of Mammals exhibition hall, U. S. National Museum.

TUESDAY, JUNE 23

8:30 AM—Morning Session

14. Analysis of some methods of trapping small rodents. Frank B. Golley, University of Georgia, Athens.
15. Spatial and homing consequences of the introduction of aliens to semi-natural populations of prairie deer mice. C. Richard Terman, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine, and Michigan State University, East Lansing.
16. Use of behavioral characteristics in evaluating morphological criteria for the generic classification of *Lissonycteris*. Barbara Lawrence, Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts.
17. Behavior of barren ground caribou on their calving grounds. Antoon de Vos, Ontario Agricultural College, Guelph.
18. Preliminary studies on the initial orientation of *Peromyscus gossypinus* in homing experiments. James V. Griffo, Jr., University of Florida, Gainesville.
19. The Barbary sheep—America's new big game mammal. Herman A. Ogren, Roy, New Mexico. (Read by Fred S. Barkalow.)

Group Photograph, South steps, Natural History Building, U. S. National Museum

10:40 AM—Annual Business Meeting, Election of Officers

1:00 PM—Afternoon Session

20. A revision of the wood rat *Neotoma stephensi*. Donald F. Hoffmeister and Luis de la Torre, University of Illinois, Urbana.
21. Another line of evidence on suprageneric relationships within the Sciurinae. Joseph C. Moore, American Museum of Natural History, New York.
22. Serum protein electrophoresis of North American mammals—progress report. Murray L. Johnson, Puget Sound Museum of Natural History, Tacoma, Washington, and Merrill J. Wicks, Director, Tacoma-Pierce County Blood Bank.
23. The status of the house shrew, *Suncus murinus*, on Guam, M. I. Kyle R. Barbehenn, National Institute of Mental Health, Bethesda, Maryland.
24. Progress report, genera of Recent mammals of the world. Ernest P. Walker, Washington, D. C. (Read by Kenneth I. Lange.)
25. Geographic variation in the eastern chipmunk. D. P. Snyder, University of Massachusetts, Amherst.
26. Shrinkage, a factor in the measurement of muskrat skulls. Maurice M. Alexander, State University, Syracuse, New York.
27. Systematics of North American lasiurine bats. E. Raymond Hall and J. Knox Jones, Jr., University of Kansas, Lawrence.

6:00 PM—Banquet, John Wesley Powell Auditorium, Cosmos Club

After-dinner program: Slides, "African Mammals," George Treichel, Conservation Foundation, New York.

WEDNESDAY, JUNE 24

8:30 AM—Morning Session

28. Development of young fox squirrels (*Sciurus niger rufiventer*). Victor H. Cahalane, New York State Museum, Albany.
29. The use of the lens to determine the age of mammals. Rexford D. Lord, Jr., Illinois Natural History Survey and Illinois Department of Conservation, Urbana.
30. Reproductive cycle of the cotton rat, *Sigmodon hispidus*. Howard Haines, University of Texas, Austin.
31. Problems of overwintering in the Arctic ground squirrel. William V. Mayer, Department of Biology, Wayne State University, Detroit, Michigan.
32. Seasonal changes in the weights of woodchucks. Robert L. Snyder, J. J. Christian and David E. Davis, Johns Hopkins University, Baltimore, Maryland.
33. Histology of the gastro-esophageal junction in representative microtine rodents. Lyle C. Dearden, University of Southern California Medical School, Los Angeles.
34. Comparative aspects of echolocation in bats. Alvin Novick, Yale University, New Haven, Connecticut.

10:50 AM—Final Business Meeting

1:30 PM—Conducted tour of National Zoological Park

THURSDAY, JUNE 25

8:30 AM—Guided tour of U.S.F.W.S. Patuxent Research Refuge, Laurel, Maryland

DIRECTORS' MEETING

The Board of Directors convened at 8:00 PM June 21, 1959, in Room 128 of the Harrington Hotel. Minutes of the previous meeting were read and approved. The Secretary-Treasurer presented the following changes in the membership list: 162 applications for membership, 77 resignations, 7 deaths, 33 delinquent for three consecutive years. Removal of the latter from the rolls was approved. In order to even the work load in the executive office it was approved to change the statistical year from December 31 to March 31. It was noted that total memberships as of June 1, 1959, were 1,682 with 561 active subscriptions, for a total mailing list of 2,185. The report of the financial audit of the Society was read and approved. The report of the Editorial Committee was read and approved, and the Editor and Secretary-Treasurer were authorized to negotiate a new contract with the Allen Press.

The following budget was adopted for 1959:

Expenses of the Journal of Mammalogy	$10,000.00
Expenses of the Executive Office	2,000.00
Editorial expenses	150.00
Membership Committee expenses	50.00
Index Committee expenses	35.00
Honoraria	200.00
AIBS	200.00
Zoological Record	100.00
Audit	35.00
Contingent Fund	430.00
Total	$13,200.00

W. P. Harris was reappointed to a new term as Trustee. Bryan P. Glass was reappointed Secretary-Treasurer. Richard H. Manville was reappointed Editor. The Board approved a recommendation that the Society plan for meeting places two years in advance. Transfer of $889.75 from the J. A. Allen Memorial Fund and $2,507.47 from the Endowment Fund to the Secretary-Treasurer for publication of the Journal was authorized. Transfer of $1,821.81 derived from life membership payments to the trustees for investment was authorized.

Amendment of RULE III to read, "Members whose dues are in arrears shall not be entitled to receive the *Journal of Mammalogy*," was recommended for approval by the Society.

Hoffmeister (Chairman), Peterson, Kelson and Glass were appointed to a committee to consider offers from reprint corporations to republish out-of-print editions of the Journal, and authorized to negotiate a contract which would serve the best interests of the Society.

ANNUAL BUSINESS MEETING

The first session of the annual business meeting was called to order at 10:40 AM, June 23, with 99 members in attendance. Minutes of the previous meeting were read and approved. The names of 162 applicants for membership received since the last meeting were presented and approved. The deaths of seven members were announced: Alex W. Blain, Angus H. Booth, P. F. English, Robert T. Moore, John T. Nichols (Charter Member), Edward L. Rabb and Malcolm R. Thorpe.

The following statistical summary of memberships and subscriptions was presented:

		Minus	*Plus*
Membership			
Changes since last report:			
Nominees			168
Resignations		75	
Deaths		7	
Dropped—delinquent		31	
		113	168
Net change	+ 55		
Status of members as of Dec. 31, 1958:			
Honorary			6
Life			108
Honorary and Life			3
Emeritus			7
Annual			1,365
Delinquent			93
Total			1,582
Subscriptions			
Changes since last report:			
Cancelled			33
New			36
Total			579
Net change	+ 3		
Mailing List:			
Total membership			1,582
Members not receiving Journal			-104
Members receiving Journal			1,478
Total paid subscriptions			579
Total mailing list			2,057

The financial report was presented and approved. The audit report was read and approved. The following agreement, read by the President, was greeted by a standing vote of thanks:

AGREEMENT

It is agreed by the undersigned, namely, Brazier Howell and the American Society of Mammalogists, that the former will donate to the latter a sum of three thousand dollars ($3,000.00) from the income of which an annual award of one hundred dollars

($100.00), to be known as the BRAZIER HOWELL AWARD, shall be made to the member, not yet having received the Doctor's Degree, who submits the most meritorious paper to a committee of three appointed by the President, for ranking submitted papers intended for presentation, in person, at the ensuing annual meeting.

Signed: ROBERT T. ORR BRAZIER HOWELL
President, American Society of Mammalogists
Dated: June 22, 1959

The amendment to Article II, Sec. 1, of the Bylaws, pertaining to Emeritus Members, that was published in Vol. 40 (1) of the Journal was approved by unanimous vote.

The entire incumbent slate of elective officers was reelected for another term. Directors elected to hold office for the 1959–61 term were: Viola S. Schantz, J. K. Doutt, Keith R. Kelson, Antoon de Vos and Victor H. Cahalane.

The report of the Editor was presented and approved. Winners of the honoraria for 1959, John J. Stephens III and William H. Adams, Jr., were formally announced by S. D. Durrant. The report of the Committee on Bibliography was approved, and the Committee was asked to prepare a recommendation pertaining to the advisability of continuing to purchase reprints of the published lists. The report of the Committee on Conservation of Land Mammals was circulated among the membership, without formal action. The reports of the Committees on Nomenclature and Index were presented and approved.

At the final business session at 10:00 AM, June 24, a total of 97 members were present. The recommendation of the Directors that RULE III be amended to read, "Members whose dues are in arrears shall not be entitled to receive the *Journal of Mammalogy*," was approved. The reports of the Membership Committee and the Committee on Marine Mammals were approved.

The Committee on Honorary Memberships proposed the names of Francis Harper and Nagamichi Kuroda for election. Both were elected unanimously.

The Pacific Lutheran College, Tacoma, Washington, was selected as the site for the 1960 annual meeting and Urbana, Illinois, was tentatively selected for 1961. Note was taken of the fact that under present rules selection may be made only one year in advance. Keith Kelson reported as representative to A.A.A.S. and N.R.C. and Harold Coolidge reported as representative to I.U.B.S. The Resolutions Committee presented the following resolutions:

WHEREAS, The Bureau of Sport Fisheries and Wildlife has filed application with the Bureau of Land Management of the Department of the Interior for withdrawal of approximately nine million acres of land for use as an Arctic Wildlife Range for the preservation of wildlife and wilderness resources in northeastern Alaska, and

WHEREAS, This area, of which over five million acres were formerly withdrawn as part of Public Land Order 82, is a refuge for caribou, grizzly bear, polar bear, Dall sheep, wolverine, and countless flocks of over 100 species of migratory birds, and is, therefore, an area of wilderness resources unique in North America, and

WHEREAS, The Honorable Fred A. Seaton, Secretary of the Interior, in a statement before the House of Representatives Committee on Interior and Insular Affairs has referred to the Arctic Wildlife Range in Alaska as the major item of legislation presented by his department in the fish and wildlife field, and

WHEREAS, An opportunity now exists, which may be lost in the future, for preserving a unique, working laboratory for the study of Arctic wildlife; therefore be it

Resolved, That the American Society of Mammalogists commends Secretary Seaton for his presentation of this legislation and urges prompt and favorable action on it.

WHEREAS, The United States Department of Agriculture and associated state agencies have begun chemical treatments within an over-all area of some 27,000,000 acres of the Southeast with the hope but dubious likelihood of exterminating the imported fire ant, and

WHEREAS, Much of this treatment consists of aerial distribution of heptachlor or dieldrin at 2 pounds of active ingredient per acre, which is equivalent in killing power to certain forms of fish and wildlife of up to 40 pounds of D.D.T. per acre, and

WHEREAS, It has already been demonstrated that one or two pounds of dieldrin per acre causes serious depletion of many kinds of terrestrial and aquatic life, and applications of one to five pounds per acre of the much more investigated D.D.T. are known to cause serious depletions of many kinds of invertebrates, fishes, amphibians, reptiles and birds, and
WHEREAS, These poisons remain toxic up to three years and may be carried into waters of all types long after application, and
WHEREAS, Extermination of fire ants will require treatment of all types of infested land including natural areas, and
WHEREAS, The Southeast possesses a wealth of fish and wildlife resources of incalculable commercial, recreational and scientific value, and
WHEREAS, The Southeast also possesses hundreds of kinds of fishes, amphibians, reptiles, birds and other animals that occur nowhere else in the world and many of these animals occupy only small areas and therefore might readily be completely exterminated, and
WHEREAS, Each of these endemic animals has such great scientific and educational value that its extinction would be a tragic loss inconsistent with the aim of the American people to maintain all harmless kinds of animals insofar as humanly possible, and
WHEREAS, The imported fire ant is listed among the twenty worst insect pests by only two of the southeastern states, and recent studies have revealed that this ant rarely eats crop plants but is primarily predaceous on other insects; therefore be it
Resolved, That the American Society of Mammalogists, through its appropriate officers, recommend to the Secretary of Agriculture, to the Chairman of the Appropriations Committee of the U.S. House of Representatives: (1) that *aerial distribution* of heptachlor, dieldrin and equivalent poisons for extermination of fire ants or other purposes *be ceased at once* before irreparable harm is done; (2) that all applications for control of fire ants be limited to treatment of individual ant mounds by ground equipment; (3) that the Department of Agriculture and associated organizations launch intensive research designed to discover pest-control methods that will not endanger desirable native animals, whether game or non-game; (4) that thorough studies be made of the effect of current control programs on fishes, amphibians, reptiles, birds, mammals and the types of animal life on which these depend for food, as well as the effects of these programs on organisms that are responsible for proper functioning of the soil; and (5) that all plans for future control programs be formulated only after great weight has been given to the possibility of extermination of any kinds of native plants and animals, especially animals and plants that are of extremely limited distribution; and be it further
Resolved, That the American Society of Mammalogists stands ready at all times to provide any federal, state or local government agency with information on mammals that is of especial scientific significance in any given area.

WHEREAS, The preservation of a segment of the remaining true prairie is in the interests of the people because of its scientific, historic, aesthetic and educational values, and
WHEREAS, The Advisory Board on National Parks has recommended to the Secretary of the Interior the establishment of the True Prairie National Park of approximately 34,000 acres in the Flint Hills of Kansas; therefore be it
Resolved, That the American Society of Mammalogists commends the stated action of the Advisory Board on National Parks and recommends to the Secretary of the Interior the early establishment of the True Prairie National Park.

WHEREAS, The many scenic, ecological and biological features of land and sea scapes constitute one of the major natural resources of the nation, and
WHEREAS, Of the 3,700 miles of Atlantic and gulf coast shoreline only approximately 270 miles, some 6½ per cent, are available to the public, and of these only half are encompassed within Acadia and Everglades national parks and the Cape Hatteras recreational area, and
WHEREAS, The Cape Cod region constitutes a unique natural area but is being threatened with commercial exploitation; therefore be it

Resolved, By the American Society of Mammalogists, that the still-unspoiled great beach portion of Cape Cod be protected and preserved for the enjoyment of the present and future generations by the creation of a Cape Cod National Seashore.

WHEREAS, It is a moral obligation of a civilized people to administer its resources on a multiple-use basis in order to secure to itself and to future generations certain important benefits, and

WHEREAS, The creation of a Wilderness Preservation System would be an important step in securing to the public, on a sustained basis, the maximum recreational, scenic, scientific, educational and historic values from specified areas; therefore be it

Resolved, That the American Society of Mammalogists, meeting in Washington, D.C., June 24, 1959, endorses the adoption by the Congress of a national policy and program such as that embodied in the proposed Wilderness Preservation System, and urges the 86th Congress for this purpose (1) to strengthen the currently introduced Wilderness Bill on which extensive hearings have already been held, notably those provisions of Section 3(c) that make it possible that those values intended to be secured in perpetuity may be jeopardized by fiat decision; and (2) to enact this strengthened measure as promptly as possible; and be it further

Resolved, That copies of this resolution be provided to the Chairmen of U.S. Senate and House of Representatives Committees on Interior and Insular Affairs, the Secretaries of Agriculture and the Interior, and the heads of the U.S. Forest Service, the National Park Service, and the Fish and Wildlife Service.

WHEREAS, The United States National Museum and its staff members comprising the local committee on arrangements have made the 39th Annual Meeting of the American Society of Mammalogists in session at Washington, D.C., June 21–25, 1959, especially significant by providing a unique historical brochure, a banquet of import to mammalogists, an extensive program for wives and children of members and, by all their diligent efforts and untiring hospitality, have made the members of the Society feel like honored guests; therefore be it

Resolved, That the Society extends its sincere thanks and appreciation to the United States National Museum and to the Fish and Wildlife Service, and especially to Miss Viola S. Schantz, General Chairman, and to the Chairmen of the local committee and to the committee members for their efforts which have resulted in making the 39th Annual Meeting a singularly successful one.

D. H. Johnson presented a special report from the Committee on Bibliography, to wit:

1. That the standing order for 100 reprints of each section of Recent Literature be discontinued after the end of the current volume.
2. That in order to continue necessary checking and reference files, the Committee be provided with either two sets of page proof or four copies of the printed Journal for each section of Recent Literature published in the future.
3. That the Committee be authorized to liquidate the present stock of reprints in the manner that it deems most profitable to the Society and most useful to individual members.

The report was approved. The report of the Committee on Conservation of Land Mammals was approved. The meeting adjourned at 12:45 PM.

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